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AT

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No. 1. — *Contributions to the Morphology of the Turbellaria.* — I. *On the Structure of Phagocata gracilis, Leidy.* By W. M. Woodworth.[1]

In the fall of 1887, Mr. H E. Valentine of West Somerville, Mass., brought to the Embryological Laboratory of Harvard College some planarians, with the suggestion that they might be infested with parasites. The planarian proved to be the interesting Phagocata gracilis of Leidy, and the supposed parasites were the pharynges of the complicated digestive apparatus. At the suggestion of my instructor, Dr. E. L. Mark, I undertook the study of this curious Triclad.

The animal, which was afterwards named by Leidy Phagocata gracilis, was first described by S. S. Haldeman ('40, p. 3) in 1840, under the name of Planaria gracilis: "Body oblong, suddenly tapering to a point posteriorly: sides nearly parallel; head square in front, with a projecting appendage on each side: neck narrowed; eyes (two) situated on each side of the narrower part; these are oblong and white, with a black dot at their internal side: ventral opening less than one third the entire length from the posterior extremity, and from this opening an intestine is sometimes protruded. General color fuliginous, veined with black. Length, $\frac{3}{4}$ in., breadth, $\frac{1}{10}$. Hab. springs in Eastern Pennsylvania."

In 1848, Leidy published a further description of the species, giving to it the name of Phagocata ('48, p. 248), because, as he says, "I detected such a remarkable peculiarity in the digestive apparatus as led me to investigate its anatomy in detail, and to form for it a separate sub-genus, characterized as follows: —

"*Phagocata,* oblonga, plano-convexa, nuda, contractilis, mucosa, antica auricularia. Aperturæ duæ, ventrales, ad os et ad generationem pertinens. Proboscides multæ.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXIV.

No. XXIII. of these Contributions appeared in the Proceedings of the American Academy of Arts and Sciences, Vol. XXV., under the title, "Preliminary Notice on Budding in Bryozoa." By C. B. Davenport.

"*P. gracilis,* nigricans, lateribus parallelis, postero acuto abrupte, plerumque antico recto; oculis duobus. Long. 9 lin., lat. 1 lin. Habitat in fontis Pennsylvaniæ.

"*Description.* Oblong, limaceform, naked, convex superiorly, flat inferiorly, very contractile; sides ordinarily parallel, convex when the animal is in a contracted state, convergent anteriorly when elongated; anterior extremity with a lateral triangular auricular appendage, straight in front, by contraction becoming convex or concave; posterior extremity abruptly pointed; ocelli two, anterior, composed of an oblong, semitransparent (nervous?) mass with an intensely black dot of pigmentum at the internal posterior part; ventral apertures two; oral aperture a little less than one third the length of the body from the posterior extremity. Color black or iron gray, and in some younger specimens latericeous."

I have quoted Leidy's description in full, because it seems to me that the first description of so striking and aberrant a species is of uncommon interest.

It is noteworthy, that, notwithstanding the faithfulness of the description, and the remarkable peculiarities of the worm, no mention of the species has been made for over forty years. It is also strange that Girard should have been ignorant of the existence of Leidy's paper, for in his list of North American fresh-water Planariæ ('51, p. 264) he uses the name proposed by Haldeman, "Planaria gracilis," and says that it is "common about Cambridge in pools and rivulets." He adds, in a note, "Planaria gracilis and very likely Planaria tigrina will not remain in the genus Planaria as soon as we shall know their internal structure." In a subsequent paper ('51ª, p. 2), "Die Planarien und Nemertinen Nord-Amerikas," the species is described under the name given to it by Leidy, but no mention is made of the most striking characteristic discovered by that observer, — the multiplicity of the pharynges.

The structural peculiarities of Phagocata were not simply ignored, they were even denied by no less an authority than von Siebold, who explained the "proboscides" of Leidy as so many processes from the lip of one normal pharynx. After quoting the description, he says ('50, p. 389): "Das erwachsene Thier soll 23 Rüssel haben, die es beim Fressen alle hervorstreckt; Ref. vermuthet, dass der Rüssel eine trichterförmige ausgezackte Mündung besitzt, und dass die beweglichen Fortsätze des Rüsselrandes für ebenso viele einzelne Rüssel gehalten worden sind."

Diesing, like von Siebold, was incredulous; in his "System," he says ('50, p. 207), "Œsophagus protractilis multi partitus (proboscides multæ Leidy)." Twelve years later, in the "Revision der Turbellarien," he writes ('62, p. 506), "œsophago multipartito."

Stimpson ('58, p. 23) in his Prodromus apparently followed Diesing, for he says "œsophago protractili multipartito."

Recently, Professor Leidy ('85, p. 49) has figured Phagocata gracilis in a popular account of "Planarians." These are the only descriptions of Phagocata I have been able to find.

Phagocata gracilis, Leidy.

When viewed from above, the general form of the animal is elongated; its lateral margins are nearly parallel, being slightly convex posteriorly; the widest part of the body is in the pharyngeal region. The largest specimens measure 30 mm. in length by 4½ mm. in breadth. Anteriorly the sides converge slightly up to about the region of the eyes, where the diameter increases, thus forming the so called head. This bears the lateral auriculate appendages. The lateral appendages are rounded, rather than triangular as described by Leidy; they are continuous with, and in fact form part of, the anterior extremity; posteriorly, the sides converge to a point (Fig. 20 *a*). The eyes appear as two elongated oval white spots, with black pigment on the internal edge. They are situated on the narrow part or "neck."

Haldeman and Leidy have described the head as being "straight in front." This appearance is seen only when the animal is at rest. It is then much contracted in the direction of its antero-posterior axis, and is usually much distorted; at such times it often appears as a shapeless black lump, this condition probably being a means of protection (Figs. 20 *b* and 20 *c*). When in motion the anterior extremity is usually convex, but not always, for it may be straight, sinuous, or concave; these shapes are only temporary, following each other in quick succession. The head changes its form especially when the animal approaches some object; for this part of the body is functional as an organ of touch; that it is suited structurally to be a kind of feeler will be evident from the description of the nervous system which follows.

Phagocata gracilis has a shiny black appearance when viewed by reflected light, but by transmitted light it is of a greenish gray color. The color may vary from black to a reddish brown on the one hand, or to a light gray on the other. I have seen small specimens which were almost milky white. The ventral surface is of lighter color than the dorsal, and there are light areas about the ventral apertures. The pigment is densest in the dorsal median line, where it forms a dark band; it diminishes toward the sides of the animal, the edges of which are quite destitute of it. The distribution of the pigment in the head region presents many variations. In most cases the posterior borders of the auriculate appendages show two light spots, and there is a third one, somewhat triangular in shape, at the anterior end in the middle line. The marginal area of the head, like that of the body, is free from pigment. Sometimes the whole head region is light with the exception of the middle line between the eye spots, where there is an extension of the dark median band previously referred to. Light non-pigmented areas occur wherever there has been a reparation of the tissues resulting from injury.

By an examination of the animal in the natural condition, only a few of the internal structures can be identified, because of the large amount of pigment present. When viewed from above, the most striking feature is a large oblong light region, the pharyngeal cavity with its contained pharynges. Immediately behind this a similar but smaller spot marks the position of the penis. From the ventral side the nervous system may be dimly seen as two long whitish bands united by transverse commissures and coming together in the head region in a bilobed enlargement, the brain. Leidy apparently confused these structures with the excretory organs, no trace of which can be seen on the living animal. He says ('48, p. 250): "There appears to be nothing peculiar about the arrangement of the blood-vessels, if such they be: the term being applied to two semi-transparent lines passing along each side of the ventral surface, and a third along the middle of the dorsal surface, the three freely communicating with each other by transverse lines and numerous smaller branches, the whole forming an extensive reticulation upon the surface of the body. At the anterior part of each ventral line, I distinctly observed a dilatation to exist." And again: "I could detect no traces of a nervous system." The two "semi-transparent lines" are without doubt the longitudinal nerve trunks, and the "dilatations at the anterior part of each," the lateral enlargements of the brain. What he means by the "third" line "along the dorsal surface," I cannot say. When sexually mature individuals are subjected to pressure, parts of the vasa deferentia and oviducts can also be made out.

Phagocata differs from all other Triclads in possessing many pharyngeal tubes instead of one. All the pharynges lie in a common chamber, and when protruded reach the exterior through a single orifice, but they open into the intestinal cavity separately. One of these pharynges, like the single pharynx of other Triclads, joins the intestine at the junction of its main trunks; the others are connected with the inferior median surface of the lateral trunks (Plate II. Fig. 20). The odd median pharynx is largest, and therefore most prominent of all. The others, which arise from the intestine farther back, are successively shorter, as well as narrower, the more remote they are from the median proboscis. The attachment of the smallest ones is about as far from the posterior end of the animal as the attachment of the chief one is from its anterior end, so that the chamber which they all occupy embraces the middle half of the body. Although there are about as many pharynges attached to one of the lateral trunks of the intestine as to the other, they are not arranged in pairs, nor have their positions any definite relation to the side branches of the intestine which open into the lateral trunks. The pharynges are rather less numerous than the side branches; they sometimes arise opposite to a branch, sometimes opposite to a space midway between two branches, or at other intermediate points. The foremost of the lateral pharynges is often considerably in advance of the corresponding proboscis of the opposite side of the body (Fig. 20). Leidy ('48, p. 249) has well described the appearance and action of the pharynges in the living animal. He says: "They are considerably longer, but narrower, than in *P. lactea*, and when not in use are packed together within the animal, so that, when the latter is placed beneath the microscope and slightly compressed, they will be seen pressing upon one another in such a manner that, if one changes its position, it will be instantly occupied by another. Those which are formed last are smallest, but they soon gain their full size. If one of these animals be punctured or cut, one or more of the proboscides will be instantly protruded as if they existed under pressure, and will move about in all directions, appearing as if entirely without the control of the animal; or if one of the animals be crushed between two slips of glass so that the proboscides will be torn from their attachment, they move about involuntarily, always in a line forwards or towards the mouth. . . . In this progressive course they constantly contract and dilate; the mouth opens, and any matter in its vicinity rushes in, when it is closed and the matter passes onwards, and by the alternate contraction and dilatation of different parts of the same tube it is thrown backwards and forwards several times, and finally violently expelled at the torn extremity. When they have escaped from the ruptures of the tegument produced by crushing, or when snipped off with a pair of scissors whilst the animal is feeding, they will present the same curious phenomena. In fact, these curious independent movements caused me at first to mistake the organs for viviparous young, and it was not until I had frequently observed the animal feeding, and examined its structure beneath the microscope, after having fed them upon colored food, that I was convinced of their true nature."

It was these automatic movements of the detached pharynges that at first led me also to believe that they were parasites. They appear as long, white worm-like bodies, one end being truncated, the other ragged and uneven, where it was torn from its attachment. They move about quite rapidly by means of the cilia with which they are covered, and waves of contraction continually pass along the length of the tube from the truncated to the ragged end. The mouth end may be greatly expanded so as to form a funnel-like structure, or it may be so contracted as to obliterate the lumen. I did not succeed in satisfying myself of the real nature of these structures until I examined one of the animals while it was feeding. I placed one of the Lumbriculidæ in a watch-glass with a Phagocata, which soon attached itself to the annelid by throwing out its many pharynges, some of which were wrapped about the victim, while others were thrust into its body (Plate II. Fig. 13). The soft parts of the prey were rapidly sucked up and swallowed by means of the peristaltic motions of the pharynges, so that in a short time there was left nothing but the empty and shrivelled integument.

By far the best reagent for killing is hot corrosive sublimate. An excess of the salt is added to the saturated aqueous solution and the whole is heated to the boiling point. A very strong solution can be prepared in this way, as the salt is more soluble in hot water than in cold. Kennel ('88, p. 455) has recommended the use of 50% nitric acid. I have used with entire success a modification of his method, viz. a cold saturated solution of corrosive sublimate in 50% nitric acid. The worm is placed on a plate in as little water as possible, and when properly extended the fluid is quickly poured over it. After a few minutes' immersion the fluid is replaced by a saturated aqueous solution of corrosive sublimate, in which the worms remain for half an hour and are then washed. I know of nothing else that will kill so quickly, and at the same time leave the tissues uninjured. For the study of the intestinal tract, unstained specimens were cleared in clove oil. The amount of pigment so obscures the organs lying beneath, that the ramifications of the intestine could be traced only on cleared specimens in which the intestine contained dark-colored food matter. For staining, Grenacher's alcoholic borax carmine followed by differentiation with acid alcohol proved to be the most useful and reliable method. I have stained both *in toto* and on the slide. Good sections for topographical study were obtained by staining in alcoholic borax carmine for 24 hours and cutting in the horizontal plane sections 30 μ in thickness. By thus lightly staining, the nerve tissue takes none of the color, and in such comparatively thick sections the finer branches show as white lines against a red background. Orth's picrocarminate of lithium is a valuable reagent on account of the selective action of the picric acid for all glandular tissue, which it brings out in sharp contrast to the red color of the other tissues. I have used this reagent also with excellent results for macerating. The affinity of hæmatoxylin stains for formed substances renders them of little use; their intense reaction with the great number of glandular structures tends to obscure results. For isolation preparations, the best results were obtained by macerating directly in the stain. I also used successfully the osmic-acetic method of maceration on fresh material. The isolated living pharynges were killed in hot 1% silver nitrate for the purpose of demonstrating the epithelium. Depigmenting was accomplished by the use of a 1% solution of potassic hydrate which was allowed to act for a few minutes on sections fixed to the slide with Schällibaum's clove-oil collodion fixative.

Cilia are present over the whole surface of the animal. In material that had been prepared in hot corrosive sublimate, the middle region of the ventral surface, where the hypodermis is thinnest, was often destitute of cilia. Likewise at the lateral edges they may be wanting. These conditions are, however, due to the action of the reagent, since in the living animal cilia are always present in these places. At the anterior end of the body on either side of the head, the cilia are somewhat longer than elsewhere. They attain their greatest length at that portion of the margin of the head which forms the auriculate projections. From the middle of each projection they gradually diminish in length until, at the anterior tip of the body and at an equally distant point behind the auricles, they are reduced to the normal length. These two areas covered by the longer cilia probably correspond to the "Tastorgane" of Iijima ('84, p. 366), and are directly related to local modifications of the hypodermis.

I cannot find either the short immovable hairs or the long "Geisselhaare" seen by Iijima in other Triclads at the anterior margin midway between the areas of the "Tastorgane"; nor have I found in Phagocata that the cilia in the head region move in different directions, as Minot ('77, p. 407) has observed in the case of other fresh-water planarians.

There has been a difference of opinion among writers as to the possibility of certain regions of the body being normally destitute of cilia. Metschnikow ('66, p. 436) and Kennel ('79, p. 125) found cilia covering the whole surface in Rhynchodesmus and Geodesmus, but Zacharias ('88, p. 542) states that the dorsal surface of a variety of Geodesmus is bare, and Vejdovsky ('90, p. 132) maintains the same for Microplana, the cilia in the latter cases being confined to the ventral surface or sole. It seems to me, however, that Moseley ('74, p. 118) long ago offered a satisfactory explanation of the condition, by saying that in Bipalium the cilia on the dorsal surface of land planarians, being weaker through comparative lack of function, are consequently more easily destroyed by the action of the reagents used in the preparation of the material. Considering the habits of land planarians, and especially the dissimilar conditions to which the dorsal and ventral surfaces are subjected in regard to moisture, exposure, contact, etc., it is not strange that the conditions of the cilia of the different surfaces should be unlike. Iijima ('84, p. 366) states that it is the exception for the edges of Dendrocœlum lacteum to be ciliated, and that the almost constant absence of cilia is due to certain parasites (Trichodina). He also speaks of a species of Geoplana from South America in which the cilia of the dorsum are replaced by a granular crust. I believe that in planarians there is primarily no localization of the cilia, and that all non-ciliate conditions are secondary.

I could nowhere find a *cuticula*. The superficial portion of the cells of the hypodermis takes a somewhat deeper stain than the body of the cells, but there is no sharp line of demarcation between the two; the color of the superficial portion fades gradually into that of the body of the cell. A true cuticula such as that described by Minot ('77, p. 407) and Loman ('87, p. 69) for Triclads, and by Keferstein ('68, p. 16) for Eurylepta, is wanting, and there is only a thickening, a condensation, of the superficial plasma of the hypodermal cells.

The *hypodermis* has proved to be the most difficult of the tissues to study, because of the minuteness of its elements, and the enormous number of dermal rods, or rhabditi, which so obscure the true conditions that it is only after long and patient study of thin sections and of macerated material that one can learn what the true characters of this tissue are.

The hypodermis is thickest on the dorsal surface; it becomes thinner toward the edges of the body, and in passing around to the ventral surface it still continues to become thinner as far as the middle line, where, forming part of the floor of the pharyngeal cavity, it reaches its greatest attenuation. There are hypodermal thickenings around the oral and genital openings, and also over two sensory areas on the ventral surface of the head region, which will be described in another place.

It is almost impossible to find a region where the cells of the hypodermis are not modified by the presence of the dermal rods. In order to get at the natural appearance of the cells, it is necessary therefore to study them in young specimens, and in the region where the rods are fewest; this region I have found to be near the margin, on the dorsal side. Very thin cross sections of young individuals are the most favorable ones for this purpose.

The cells are columnar, the height necessarily varying with the thickness of the hypodermis. The nuclei are large, have an irregular or sinuous outline, and are situated, as a rule, near the bases of the cells (Figs. 1 and 2). This position is not constant, and depends upon the number and influence of the rhabditi that are present. There is no nucleolus proper, the chromatin being scattered through the nucleus in many large granules. The size of the nucleus does not appear to depend upon the size of the cells; for while the cells in different regions vary to a great extent, the nuclei remain of nearly uniform size.

The cells are finely striated; the striations are most prominent at the basal ends of the cells, and cannot be traced to their free ends. Such radial striations have been described by Böhmig ('86, p. 294) in the hypodermis of Graffilla, and more recently by Lippitsch ('90, p. 328) in the epidermal cells of Derostomum. Iijima ('84, p. 369) also alludes to fine striations in the epidermal cells of Planaria polychroa. The cells do not "etwa flach auf die Basalmembran aufsitzen," but are connected with it by fine processes "welche etwa kammförmig ziemlich dicht neben einander stehen." These processes he believes to be directly continuous with the striations of the cells, and to be protoplasmic prolongations of the cells. He traces them through the basement membrane into the muscles below, thus establishing "eine organische Verbindung zwischen dem Epithel und den Körperinnern." His figure (Taf. XX. Fig. 4) is confusing, and in addition was drawn, as he admits, from a specimen in which the basement membrane exhibited pathological conditions. Besides the striations in the cells, there appear creases or folds resulting from the pressure of the rhabditi.

In thick sections through regions where the rhabditi are numerous, the epidermal cells have the appearance of being joined to the basement membrane by foot-like processes. This appearance at first led me to believe in a condition like that described by Iijima, and it was only after studying sections of material in which the rhabditi had been removed (Fig. 3) that I understood their relations to the cells.

The rhabditi do not lie *in* the hypodermal cells, but *between* them. Kennel ('79, p. 126) and Braun ('81, p. 305) are the only observers who have described them as having an *inter*cellular position. It will be seen from the following description of their development in Phagocata, that such a position is the only natural one. The presence of these rods between the cells produces a crowding, and the pressure is so great that it causes the cells to become displaced and much modified in shape. The nuclei may be pushed out to the free ends of the cells, or crowded down to their bases, and the cells themselves may be so reduced as to appear like mere filaments (Fig. 3). Kennel ('79, p. 126) describes the epidermal cells of Rhynchodesmus after the removal of the rhabditi, as "feine Fädchen . . . so lang als die Epidermis dick ist." Regarding their intercellular position, Braun ('81, p. 305) states for Bothrioplana that the rhabditi "nicht allein zwischen den Zellen stehen, sondern auch das Protoplasma der Zellen durchbohren." In Phagocata, as in Rhynchodesmus, the rhabditi are so numerous that the hypodermis appears at first to be entirely composed of them. As Kennel expresses it, "ausser den feinen, fadenförmigen Zellen kaum etwas anderes Platz zwischen ihnen hat." It is in thick sections, where the epidermis is many layers deep, that the bases of these compressed cells present an appearance as if the hypodermis were connected with the basement membrane by fine foot-like processes. This appearance is only seen where the rhabditi are most numerous. At the lateral edges of the body, where there are few, and where consequently the cells retain their primitive cylindrical form (Fig. 2), the latter are applied to the membrane by their broad bases. It is in these regions also that the striations previously spoken of are most distinctly seen.

Moseley ('74, p. 118) says, "The epidermis here [land planarians] is seen to be made up of large gland-cells and cells containing rod-like bodies and a certain amount of vertical filaments." "The irregular filaments which fill up the interspaces between the gland-cells and rod-like bodies appear to be the remains of the cell-walls and rod-like bodies."

He further says, "The substance of the epidermis is probably made up, in the living condition, of cells resembling the gland-cells described, but of various dimensions, and of cells containing rod-like bodies."

Since the "rod-like bodies," or rhabditi, are really modified glands, Moseley's statement amounts to saying that the epidermis is composed entirely of gland cells, a conclusion which it is not easy to adopt. Moreover, I believe that Moseley's "gland-cells" are only rhabditi that have been modified by the action of the reagent which he used for their demonstration. Kennel ('79, p. 126) obtained similar conditions by the action of chromic and acetic acids on the rhabditi of land planarians. I have found that in Phagocata by the use of picric acid the dermal rods become swollen and granular, resembling the "gland-cells" described and figured by Moseley. "The vertical filaments" were undoubtedly the true epidermal cells, reduced to a filamentous condition by the influence of the many rhabditi lying between them.

I cannot find any organic connection between the cells of the hypodermis and the deeper tissues, such as has been described by Iijima. Although appearances like those described by him do occur, they are secondary conditions, dependent on the presence of the rhabditi and the development of their mother cells. The basement membrane is everywhere traversed by fine tubular processes of the mother cells of the rhabditi, which lie imbedded in the body parenchyma. This fact, together with striations of the cells of the hypodermis and the ultimate reduction of these cells to filaments, might easily lead to conclusions such as those of Iijima. His sections were thick (10–20 μ) both absolutely and in proportion to the length of his largest specimens (20 mm.), whereas my sections were only 5–10 μ in thickness, although the worm attains the length of 35 mm.; moreover, isolation preparations were studied in connection with these sections.

The hypodermis consists of the hypodermal cells and the rhabditi that lie between them. There are no unicellular glands in it. Lang ('84, p. 49) described in Polyclads a granular "interstitial tissue" containing nuclei and pigment which arises, according to his conjecture, from a coalescence of indifferent epithelial cells. Such conditions I cannot find, nor can I detect any cement ("Kittsubstance"), such as that described by Graff ('82, p. 44) for Rhabdocœles.

The dermal rods or *rhabditi* are defined by Graff ('82, p. 49) as "die stark lichtbrechende glasartige homogenen Stäbchen, welche weder einen Faden noch einen Nadel einschliessen und durch ihre glatte Oberfläche, regelmässige Gestalt und ihren Glanz auffallen."

In Phagocata the rhabditi are found in almost every portion of the hypodermis, there being only one region from which they are altogether absent, viz. around the gonopore, where they are gradually replaced by many subcutaneous glands, which open to the exterior in a broad circular area surrounding that orifice. They are present around the oral opening, even up to the aperture, where they abruptly cease. They are most abundant in the middle line on the back, becoming gradually fewer toward the sides and anterior end, but they are again abundant on the ventral surface. They are found over the eyes, and in the epithelium of the two anterior sense organs, where they are well developed but few in number. Iijima ('84, p. 371) has stated that they are wanting in this region in the case of D. lacteum, but are present in Planocera polychroa and Polycelis tenuis. He has also shown that in the case of D. lacteum they are unusually abundant in the region of the genital orifice, both in the epithelium and in the parenchyma, and supposes that they have a sexual significance as urticating organs, the "Liebesfeile" of Schneider; but their absence in this region in Phagocata precludes the assumption that they have in this species any such function.

The rhabditi are all of one kind, but they vary in size. The variations are not local, different sizes occurring wherever rhabditi are found. Some are as long as the hypodermis cells, while others are comparatively short; they vary from $1.5\ \mu$ to $16\ \mu$ in length. There is an interesting correlation between the thickness of the hypodermal layer and the size of the largest rhabditi; those of the thin hypodermis of the ventral surface are invariably smaller than those of the dorsal side. Each is spindle-shaped, and the outer end is slightly more pointed than the deep end. They stain intensely in the carmine dyes, and then appear perfectly homogeneous; but when stained in Orth's picrocarminate of lithium with an excess of the picric acid, they take on a bright yellow color, and appear more or less swollen and distorted, according to the length of time the dye is allowed to act. Often they have the appearance of hollow capsules filled with granules, or containing a few irregular refractive lumps (Fig. 9). It was probably the swollen and altered rhabditi that Moseley mistook for gland cells. The peripheral portion of the substance of the rhabditi is not affected by the reagent as the contents are. This outward unaltered portion presents the appearance of a capsule, or thick membrane, with a double contour. Moseley says of his glandcells, "The cell appears to have a double wall, for an irregular crumpled membrane is seen often within it."

The rhabditi which lie between the hypodermal cells are not parallel, but are somewhat inclined toward each other, the outer ends generally converging about centres so as to form groups or packets. The small ones lie out near the free surface of the hypodermis; and the largest may reach the basement membrane (Fig. 1). Usually the long axes of the rhabditi are approximately perpendicular to the surface of the epidermis, but they may assume almost any angle with each other; small rods are sometimes seen lying at right angles to neighboring ones.

It was first shown by Oscar Schmidt ('48, p. 6), in 1848, that in the case of Rhabdocœles the rhabditi are developed in subcutaneous flask-shaped cells. Since that time similar conditions have been discovered in all the Triclads. Up to the present time, the development of these cells, "Stäbchenbildungszellen," has not been traced. My studies seem to throw some light on their genesis, and also to show how the rods find their way out between the cells of the epidermis. I first recognized the parent cells in isolation preparations, and saw them in sections only after depigmenting and staining the sections on the slide. Later, I obtained a fresh supply of material, and was able to demonstrate them in abundance, and in all stages of development. They are more easily to be seen on the ventral side of the animal, where they are less obscured by pigment. In their fully developed condition they lie in the body parenchyma immediately beneath the longitudinal muscles. On the ventral side, where the muscle layer is very thick, they may be found in between the strands of the muscles as well as below them. The parent cells have the form of flasks with greatly elongated narrow necks tapering off into long tubular processes, which are traceable outward through the muscles to the basement membrane, and, traversing this, are seen to open out between the cells of the hypodermis. Thus the deep-lying parent cells are in direct communication with the outer world (Figs. 1, 6, and 10). It is by means of these tubular processes that the rhabditi find their way to the exterior, and at length come to occupy positions between the hypodermal cells. I have previously pointed out that the rhabditi in the epidermis lie in groups or packets; presumably each of these groups was at one time contained in a single parent cell.

The connection of the parent cells with the epidermis is a primitive one, for they are only modified cells of the hypodermis, which never cease to retain their connection with that layer. In the earliest stages of development that I have found, they appear like small sacs imbedded in the superficial portion of the longitudinal muscle band, close to the basement membrane, with which they are connected by short necks or tubes (Fig. 4). The cell at this stage contains a single very large nucleus, in which there is no nucleolus, since the chromatin exists, as in the other cells of the hypodermis, in the form of fine particles scattered uniformly through the nucleus. Later, the cell begins to sink deeper into the tissue below the hypodermis, and the tubular neck increases correspondingly in length. The cell contents become finely granular, and appear to grow at the expense of the nucleus, which no longer fills so completely the sac, but becomes smaller and occupies the bottom of the cell (Fig. 7). In the protoplasm surrounding the nucleus, there appear small, round, highly refractive particles that stain deeply. These increase in number and in size, and soon become elongated, taking on the spindle shape so characteristic of the rhabditi (Fig. 6, *rhb.*). During these stages of formation the cell comes to lie in the body parenchyma below the muscle bands, but still retains a connection with the hypodermis by means of its long tubular process. The cells are at length filled with rods, and the nucleus is crowded to the bottom of the cell (Figs. 1, 5, and 10).

The fully developed rods are guided to the exterior by means of the tubular prolongations of the parent cell, and finally make their way through the basement membrane and come to lie between the cells of the hypodermis. The rhabditi, so long as they are contained in the parent cell, are not hard and rigid, but possess a certain amount of plasticity, as can be seen by the manner in which they are bent when many are packed in one cell. This plastic condition of the rods facilitates their passage through the basement membrane. I have been able to find a number of cases such as that represented in Figure 8, where I have shown one of the rods in the act of passing through the membrane. The rods possess this pliability until they leave the deeper tissues, and they attain their definite shape only after they reach the hypodermis, where they become hard and inflexible. After the discharge of the rhabditi, the parent cells become absorbed and disappear.

Anton Schneider ('73, p. 87) says concerning the parent cells, "Sie haben mehrere nach der Haut gehende Ausläufer, deren Epithelzellen reichlich damit gefüllt sind." According to Moseley ('74, p. 119), "The parent cells of the rod-like bodies are arranged beneath the external longitudinal muscular layer at a tolerably even depth; they are, in spirit specimens, of an elongated oval form, with the upper extremity drawn out in a point or long filament, which in some cases may be seen to reach up to the basement membrane." In another place ('74, p. 120) he says, "On treatment with potash, the cells of Bipalium swell up, are seen to contain rod-like bodies, and the fine filament at the upper extremity appears like a duct leading to the surface of the basement membrane."

Hallez and Iijima do not make mention of any processes of the sub-hypodermal parent cells, but believe that the cells are ruptured, and that the rhabditi make their way to the epidermis through the tissues of the body. Hallez ('79, p. 6) says: "Jai été temoin une seule fois de la rupture d'une cellule productrice chez Mesostomum tetragonum; il m'a été impossible de retrouver dans cette cellule rompue la moindre trace du noyau." Iijima ('84, p. 371) writes as follows: "Die Bildungszellen sind rundlich und mit einem ausserordentlich feinkörnigen Inhalt versehen." And again: "Haben die Rhabditen ihre definitive Grösse erreicht, so durchbrechen sie die Zellenwand, welche schlieslich absorbirt zu werden scheint und wandern durch den Bindgewebe und die Basalmembran entweder einzeln oder in Gruppen nach aussen in die Epidermiszellen, in denen sie definitiv verbleiben."

Not all of the rhabditi that are developed in the parent cells of the sub-hypodermal tissue find their way to the exterior. Many of the cells apparently lose their connection with the hypodermis, and their rhabditi are discharged into the body parenchyma; only on this assumption can one explain the presence of the numerous rhabditi that are found scattered in the sub-hypodermal tissues. This condition is not the normal, or at least not the original one. These often occur in large numbers in the zone immediately inside of the longitudinal muscle bands, which is occupied by the mother cells, where they lie in no definite positions, and with their axes directed at all angles.

Rhabditi of all sizes may be developed in the same parent cell. Those of different sizes are not confined to special cells, as found by Schneider ('73, p. 83) and Graff ('74, p. 128) for Mesostomum. Besides the fully developed rhabditi there are in the cells particles that have no constant form, but have the same optical appearance and stain the same as the rhabditi (Figs. 6, 10). These bodies may be either residual matter, disintegrating rhabditi, or incipient rods. They never occur in the epidermis, but are left behind after the discharge of the rhabditi, and by the absorption of the wall of the parent cell they find their way into the body parenchyma, where, with the rods previously referred to, they lie scattered about. Lang ('84, p. 52) found similar bodies along with the rhabditi in Polyclads, and speaks of them as "junge kugelige Stäbchen." I am inclined to regard them as residual secretions.

To my mind it is unquestionable that the parent cells of the rhabditi are of ectodermic origin, as first suggested by Hallez ('79, p. 7). It is only in Triclads and in Rhabdocœls that the mother cells lie in the deeper tissues, and we know so little about the embryology of these groups that we cannot tell just how the passage from the exterior takes place. I have endeavored to show that the cells have a connection with the hypodermis in the earliest stages of their development, long before they show any traces of rhabditi, but whether the cells pass from the hypodermis through the basement membrane, or are separated from the hypodermis before the formation of such a structure, I cannot say. The epidermis of embryos of Mesostomum was found by Graff ('82, p. 56) to be filled with rhabditi, while he could find no traces of the sub-hypodermal parent cells so prominent and abundant in the adult. In Polyclads, the development of the rhabditi is in my opinion identical with that in Triclads; but in the former the parent cells lie permanently in the hypodermis, whereas in the latter they sink down below that layer, where greater opportunity for growth is afforded. The condition found in Polyclads, therefore, I believe to be the primitive one.

Another mode of origin of the parent cells of the rhabditi has been proposed by Loman ('87, p. 69), who considers them to be modified connective-tissue cells that migrate from their original positions in the mesenchyma and pass bodily through the basement membrane, and come to lie eventually between the cells of the hypodermis; or, in the words of the author, "Nach meiner Meinung sind die Stäbchenzellen mesenchymatöse Gebilde, die eine factische Wanderung durch dass sie umgebende Bindgewebe unternehmen, während ihr Inhalt sich zu den fadenförmigen Stäbchen ausbildet. Endlich treten sie durch die Basalmembran (wovon später die Rede sein wird), drängen sich zwischen die Zellen der Oberhaut," etc. Thus according to Loman the parent cells form a part of the hypodermis, and only differ from the conditions found in Polyclads in that their epidermal position is a secondary one. Loman presents no evidence, and in the face of the facts here presented his position is untenable.

Rhabditi are being constantly discharged from the epidermis during the life of the individual, and provision must be made for their renewal. Parent cells are therefore being continually produced to supply the steady demand of the epidermis for rhabditi. The evidence of this lies in the fact that in individuals of all ages these cells are found in all stages of development. Iijima ('84, p. 373) says "es sicher scheint, dass die Rhabditen nicht ausgestossen werden." If the rods are not discharged from the hypodermis, why are they being continually developed throughout the lifetime of the individual? Something must become of them, or there would be an accumulation too great to find room in the hypodermis.

Kennel ('88, p. 474) says, relative to this subject: "Lässt man sie [planarians] aber in Uhrschälchen mit Wasser längere Zeit unbehelligt, so dass sie sich festsetzen, und stört sie dann plötzlich, so ziehen sie sich stark zusammen, machen heftige Bewegungen und suchen zu entfliehen. An der betr. Stelle aber findet man bei schneller Untersuchung Massen von Rhabditen in allen Stadien der Auflösung, und wenn man das Wasser schnell ausgiesst, findet man dort ein Klümpchen zähen Schleim, — die Stäbchen lösen sich in Schleim auf." I have often repeated the experiment of Kennel, and have always found rhabditi in large numbers in the slime secreted by the worm when placed on a glass plate.

We may now consider the question of the morphological and physiological meaning of the rhabditi. Two interpretations of the morphological value of the dermal rods have been given by naturalists. The larger number of observers consider them homologous with the nematocysts[1] of Cœlenterates; whereas the more recent investigators believe them to be the morphological equivalents of gland secretions. I coincide with the latter explanation, and offer the following arguments in its support. The parent cells are unicellular glands, and the rhabditi, their secretions, like the secretions of other dermal glands, are voided from the body of the individual. The rods cannot function as organs of touch in lending resistance to the epidermis, as suggested by Max Schultze and maintained by many others, for they do not lie in the epidermis cells, but between them. The insensible gradations that exist between rhabditi and the secretions of glands, as exemplified in the so called "Pseudorhabditen," "Schleimstäbchen," "Schleimblöckchen," and "Körnerdrüsen," have been to me one of the most striking evidences of the glandular significance of the rhabditi. The dermal rods of Phagocata, when acted on by reagents, present conditions resembling all the varieties of dermal bodies figured by Lang, and, as I have said elsewhere, I believe that the epidermal "gland-cells" of Moseley were only rhabditi modified by acids. Sub-hypodermal glands and the mother cells of the rods never occur together. Where rhabditi are absent, their place is taken by glands, and *vice versa*. This is illustrated in the region of the gonopore and at the edges of the body. Another proof consists in the fact that the reaction with stains is always the same for both glands and rhabditi. With picrocarmine the effect is most striking. All the tissues of the body take the carmine except the rhabditi and the glands, both of which, owing to their yellow color, stand out in contrast to the rest of the body.

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[1] According to Camillo Schneider ('90, p 375) even the nematocysts are to be considered only as highly specialized secretory cells derived from simple gland cells.

Keferstein ('68, p. 15) was the first to speak of the rhabditi as glandular secretions, and he called the parent cells "Stäbchendrüsen," and the rods "geformte Schleimmassen." More recently this view has been confirmed by Lang ('84, p. 52) and Kennel ('88, p. 474). The secretions both of the slime glands and of the accessory sexual glands often appear as rod-shaped bodies, and it was evidently this appearance of the secretions occurring around the sexual organs that led Jensen ('78, p. 11) to consider them rhabditi, and to speak of them as urticating organs functional during copulation, — the theory first suggested by Anton Schneider. Similar rod-shaped secretions are figured by Graff, who calls them "Schleimpröpfchen."

If we are to consider the parent cells as glands, what part do the rhabditi play in the economy of the worm? I must agree with Kennel, that the rhabditi are of use to the worm in securing food, and, I may add, serve also for protection. Phagocata, like all planarians, is carnivorous, and observation of its feeding habits has shown me that rhabditi are cast out of the body in large numbers, and that this condensed secretion helps to entangle and disable the prey. If one of the worms be placed on a glass plate with a very little water, it soon becomes hopelessly entangled in its own secretions, and when in this condition placed in abundant water, some minutes elapse before it can free itself and regain its activity. If some of the slime be examined with high powers of the microscope, it will be seen to contain many rhabditi, in all stages of dissolution. The rhabditi dissolve slowly in water, and it is by reason of this slow disintegration that the slime retains a thickness and tenacity that impedes the movements of an organism in contact with it long enough for the worm to lay hold of it with its many pharynges.

The conditions found in parasitic Turbellarians may be mentioned as evidence that this is the function of the rhabditi. Only four parasitic species have been studied histologically, three of which belong to the Rhabdocœles and one to the Triclads. In all of these forms rhabditi are absent, but in their stead are found sub-hypodermal glands which resemble the parent cells of rhabditi, and like them open to the exterior, — another illustration of the complementary occurrence of rhabditi and glands.

Von Ihering ('80, p. 149) states that in the case of Graffilla muricicola, from the kidneys of Murex, concretions and rhabditi are altogether wanting in the epidermis. Their function, he says, is one of protection, and hence they are not needed in a parasite. Lang ('80, p. 108) says of Graffilla tethydicola, from the foot of Tethys, that there are no rhabditi, but "Unmittelbar unter den Haut liegt eine grosse Anzahl eizelliger, birnförmiger, sich hauptsächlich mit Picrocarmine intensiv färbender Drüsen." Graff ('82, p. 375) says, concerning the same species, "Ueberdies finden sich hier unter der Haut zahlreiche einzellige birnförmige Drüsen." Anoplodium parasitica, a parasite in the body cavity of Holothuria tubulosa, also possesses no rhabditi: "Ich habe weder an frischen noch an conservirten Exemplaren von *stabchenformigen* Körpern oder von irgend einem Pigmente etwas wahrnehmen können." (Graff, '82, p. 376.)

In Planaria limuli, a Triclad ectoparasitic on Limulus polyphemus, I have been unable to find any trace of rhabditi, but have found in abundance sub-hypodermal glands that resemble the parent cells of rhabditi, and like them send long ducts to the epidermis. Graff ('79, p. 203) states regarding this species that there are no true rhabditi; but he speaks of certain "Haftorgane," which he compares to rosettes of rod-like bodies, and then adds: "Die dieselben zusammensetzenden Stäbchen (Haftstäbchen) bilden sich im Innern des Körpers in besonderen Drüsen und färben sich äusserst intensiv in Carmine und Hämatoxylin," — but I could not find these organs.

Thus we see that in parasitic Turbellarians there are no rhabditi, their place being taken by many sub-hypodermal glands. Assuming that the rhabditi are condensed secretions used in securing prey and for protection, the conditions present in parasitic forms are in every way consistent with our conclusions. The only other possible function for the rhabditi is that assumed by Graff ('82, p. 58) and stated by him as follows: "Die plausibelste Anschauung ist auch heute noch die von Schultze gegebene und von Stein auch für die Stäbchen der Infusorien adoptirte, wonach die Stäbchen indem sie dem äussern Drucke einen Widerstand entgegensetzen, in ähnlicher Weise befördernd auf der feinere Tastgefühl der Haut einwirken, wie der Nagel auf Tastvermögen der Fingerspitze." I have shown that on account of their intercellular position the rods probably cannot have such a function; but even if this evidence were considered insufficient to disprove their supposed office, one would have to encounter the objection that so important a function would not be likely to be entirely lost in parasites, particularly in such active ectoparasites as P. limuli, where the parasitism is of such a nature that sensory organs would still be of great importance in the animal's economy.

To summarize, then, *the dermal rods are to be considered as condensed secretions arising in sub-hypodermal unicellular glands of ectodermic origin. All gradations exist between rhabditi and the secretions of normal glands. The rhabditi are being continually cast out of the body, and replaced by new ones developed in new parent cells within the body parenchyma. The connection of the parent cells with the epidermis is a primitive one, and the rods pass to the exterior by means of the tubular ducts formed by the neck of the elongated cells. The rods lie between the cells of the epidermis; they are slowly soluble in water, and are used by the animal in securing food and for protection.*

The *basement membrane* is a homogeneous layer immediately under the hypodermis, the cells of which are directly connected with it. It varies in thickness in different individuals and in different parts of the same individual; 1 μ and 6.5 μ are the extremes that I have found. It stains deeply in all of the carmine dyes, and always takes a darker color than the underlying muscles. A granular condition, such as is mentioned by Iijima ('84, p. 375), does not exist, nor is there any appearance of the fibrous structure described by Lang ('84, p. 63) for Polyclads. Minot ('77, p. 408) states that the basement membrane is composed of circular fibres. The only appearance in Phagocata approaching that described by Minot is seen in surface views of bits of the membrane occurring in isolation preparations, where on one surface there appear parallel markings; but these are no doubt due to the intimate contact of the membrane with the circular muscle fibres. The membrane is closely applied to the muscle fibres, and in longitudinal sections, where the circular muscles are cut across, the inner contour appears uneven, owing to the projecting ridges which it sends into the intermuscular spaces (Figs. 4, 6, 7, and 10); stated in another way, the circular muscles may be said to indent the basement membrane, leaving their impression in the form of parallel grooves on its under surface. In cross sections of the worm, the inner border of the membrane appears perfectly smooth, and parallel to the circular muscles (Fig. 2). The only departure from homogeneity is caused by the fine channels occupied by the processes of the parent cells of the rhabditi (Figs. 1, 4, 6, 7, and 10), and these are only transitory, soon becoming obliterated. Occasionally pigment granules find their way through these openings, and may become caught in the basement membrane.

There can be little doubt that the basement membrane is a product of the hypodermis. There is a direct relation between its thickness and that of the latter; hence it is thickest on the dorsal, and thinnest on the ventral surface of the animal. It is true that the hypodermis is easily separated from the membrane, but on the other hand the intimate relation between the two structures is evident from the manner in which the cells of the former remain attached to the latter after the rhabditi have been removed by partial maceration (Fig. 3); and even when the hypodermis has been entirely removed, the outer contour of the membrane in regions where, in consequence of the presence of many rhabditi, the hypodermal cells have become much compressed, appears irregular, the uneven projections representing the points of attachment of the hypodermal cells. In those regions where the rhabditi are few or absent, the basement membrane presents a comparatively smooth surface. There is no evidence in Phagocata that the membrane is an independent cellular tissue, as in Polyclads, since no traces of structure could be demonstrated, the membrane appearing homogeneous with all of the stains that were employed. In my opinion, therefore, the basement membrane is of hypodermal origin.

The *pigment* in Phagocata occurs in the form of fine granules, of an irregular outline and of a dirty greenish color. It lies principally in the longitudinal bands of muscles between the fibres, so that, when a worm is put under pressure and viewed with moderate powers, the pigment appears as if arranged in parallel rows running lengthwise of the animal. In the deeper tissues, below the muscle bands, the pigment occurs in patches and streaks (Fig. 1). No pigment occurs normally in the hypodermis. There are no special pigment cells; the pigment occurs in the form of distinct separate granules, which are intercellular in position, never intracellular. The origin of pigment as isolated granules might be explained by some such theory as that of Eisig ('87, p. 765), by which it is to be considered as a product of the excretory system, — a kind of utilized excreta.

There are only three systems of *muscles:* the circular, the longitudinal, and the sagittal or dorso-ventral. As compared with the complicated musculature of other fresh-water planarians, that of Phagocata is much simplified, and in this respect it agrees with Gunda sementata (Lang, '81ª, p. 193) and Planaria abscissa (Iijima, '87, p. 344). The circular muscles form a single layer immediately under the basement membrane, to which, as we have seen, they are closely applied. The longitudinal muscles form a thick band inside of the circular layer, and are much thicker on the ventral side (Fig. 10) than on the dorsal (Fig. 1). In cross sections the longitudinal muscles appear separated into bundles, between which the ends of the dorso-ventral fibres are seen passing to the basement membrane, into which they are inserted. I have not been able to find a nucleus in or on either the circular or longitudinal muscle fibres. The nucleus of the dorso-ventral fibres is eccentric, as in the muscles of Planaria torva, figured by Ratzel ('69, p. 275, Taf. XXIII. Fig. 26). In cross sections both circular and longitudinal fibres have an irregular outline and show a differentiation into an outer highly refractive contractile portion and an inner feebly refractive axis (Plate I.). Branching ends were observed only in the sagittal fibres.

A reticulate *mesenchyma* constitutes the greater portion of the substance of the body, occupying all the spaces between the organs. The spaces left by the irregular network formed by the branching cells (Plate II. Fig. 18) are connected with one another, and are to be considered as a kind of pseudocœle; they are filled with a granular perivisceral fluid. The sagittal muscle fibres in some places appear to be directly continuous with branches of the mesenchyma cells (Plate II. Fig. 18, *mu. sag.*), so that by contraction of the muscles the sizes of the spaces would be altered, and thereby the perivisceral fluid would be set in motion, thus establishing an irregular circulation in the pseudocœle. Lang ('84, p. 83) maintains that in the case of Polyclads these spaces are intracellular in their origin, and that the so called perivisceral fluid is the result of a liquefaction of the plasma of the connective-tissue cells, which thus become vesicular, and finally, by the breaking through of their thin walls, form a network. But if the pseudocœlar spaces were intracellular in their origin, as claimed by Lang, it would be more difficult to understand the intimate relation between the muscles and the processes of the reticulated parenchyma cells; it would not, however, be in any way an exceptional condition for muscle fibres to be attached to the prolongations of *stellate* connective-tissue cells, more especially when we consider that the muscle fibres and mesenchyma cells have a common origin. As is well known, the Hertwigs have produced evidence to show that the mesenchymatous muscles of the Pseudocœlous animals are "besonders differenzirte Zellen der Bindesubstanz" ('81, p. 98). Moreover, the mode of origin maintained by Lang is not founded, as far as I understand it, on evidences from embryonic conditions. Graff ('82, p. 72) was unable, from the evidence found in Rhabdocœles, to establish "a distinction between muscle fibres and connective-tissue fibres"; and Hamann ('85, p. 96) has shown that in Echinoderms the connective-tissue cells are in direct continuation with the muscle fibres of mesenchymatous origin. From the study that I have made of the conditions in Phagocata I am convinced that they are like those found in Rhabdocœles.

Imbedded in the mesenchyma are the parent cells of the rhabditi and also the glands that open at the surface in different regions. There are two large accumulations of glands that open to the exterior, one around the gonopore, the other on the ventral surface of the head region. A smaller accumulation exists near the posterior end of the body. The glands that occur in the head region afford important evidence of the morphological equivalence of rhabditi-producing cells and ordinary dermal glands. The deep ends of these glands are located behind the brain, between it and the ovaries, and in passing over the brain they run downward and forward till they open out on the ventral surface of the head close to its anterior margin. They are numerous, and occur in two bundles or groups, one on either side of the median plane of the body. They appear as long sinuous tubes with enlargements or swellings occurring at intervals (Plate II. Fig. 17), but without any evidence of branching, and it has not been possible to distinguish between the gland proper and its duct. Not being uniformly distributed, the finely granular contents of the tubes cause the irregular enlargements referred to. Nuclei could not be detected in any portions of the ducts. The two bundles of glands begin immediately in front of the ovaries, and as they pass forward converge, so that when they pass over the commissure of the brain they are in contact with each other; but they soon diverge again, and make their way to the surface as already described. These two bundles of glands I believe to be the homologues of the "Stäbchenstrassen" found in Rhabdocœles, and most prominently in the Mesostomidæ. Both the position and the course of the glands in Phagocata are identical with those of the "Stäbchenstrassen" in Rhabdocœles, and the "wiederholte Anschwellungen" (A. Schneider, '73, p. 83) in the latter correspond to the repeated enlargements in the former. The glandular organs of Rhabdocœles differ from them only in the nature of their contents. Furthermore, the almost complete absence of rhabditi in the head region of Phagocata strengthens this conclusion. One has only to compare Leuckart's ('52, p. 23) description of Mesostomum and the figures given in Graff's great monograph with the conditions present in Phagocata, at once to recognize the probable equivalence of these structures. A similar but smaller accumulation of glands is found at the posterior extremity of the body in Phagocata, and it is worthy of note that there is likewise in Rhabdocœles an accumulation of rhabditi-secreting organs in the same region. The slime-secreting glands at the extremities of the body are used in Phagocata as a means of attachment, for it is principally by its extremities that the worm fastens itself to objects, as can be seen when one attempts to remove it from the side of the aquarium.

The other glands that are imbedded in the mesenchyma are those which open around the genital orifice. Together with their ducts they resemble in form the parent cells of the rhabditi; they also react like the glands of the head region with all stains. A portion of one of these glands from an isolation preparation is represented in Plate IV. Figure 41.

The *digestive apparatus* of Phagocata is like that of other Triclads, except in regard to the number and arrangement of the pharynges, which form such a striking feature of this species. The form, position, relations, etc. of these pharynges have already (p. 4) been described, and it has also been stated that at the junction of the three main tracts of the intestine there is one pharynx which is larger and more prominent than the rest (Plate II. Fig. 20, *phy. m.*), and that this is the homologue of the single pharynx of other Triclads. There is no difference in histological structure between this median pharynx and those which connect with the lateral tracts. In a cross section of a pharynx (Plate II. Fig. 12) the following layers can be distinguished, beginning from the outside: (1) the fine cilia covering the external surface, (2) the external epithelium, (3) a single layer of longitudinal muscle fibres, (4) a single layer of circular muscles, (5) a wide zone occupied by connective-tissue cells and salivary ducts and traversed by radial muscle fibres, (6) a single layer of longitudinal muscle fibres, (7) a broad band of circular muscle fibres, (8) the internal epithelium, and (9) the cilia lining the lumen (compare also the longitudinal section shown in Fig. 16). The external covering of cilia disappears at a region about two thirds of the distance from the free end of the pharynx toward its insertion on the intestine, and the epithelium there loses its smooth appearance, becoming wrinkled and creased. The cilia that line the lumen of the pharynx are more restricted in their distribution, and are lost at about one third of the way from the extremity, where the internal epithelium also becomes longitudinally folded, many of the folds projecting far into the lumen of the pharynx (Plate II. Fig. 12, *e'th. i.*). In this portion of the epithelium there are many nuclei, whereas in the ciliated region nuclei cannot be seen. Compare Figures 12 and 16, Figure 12 being a cross section which passes through the non-ciliated portion of the internal epithelium. There are no nuclei anywhere in the external epithelium of the fully developed pharynx, except near its proximal end. By the use of silver nitrate, however, I have been able to demonstrate that the layer is a true epithelium. Isolated pharynges were killed with hot 1% silver nitrate. By using the solution hot, the pharynges were killed in an extended condition. A tangential section through material treated in this way is represented on Plate IV. Fig. 47. I have been unable by any method of staining to demonstrate the presence of nuclei in these cells, the boundaries of which are so plainly brought out by impregnation with silver.

In young pharynges (Plate II. Fig. 14), where the tissues are not fully differentiated, nuclei are to be seen in both the external and internal epithelial coverings, although no trace of them can be found later on. It is not difficult to find pharynges in different stages of development, since the number increases with the age of the individual. The young pharynx begins as a solid bud of tissue projecting into a cavity hollowed out of the mesenchyma. The cavity is lined with a layer ot flattened cells, which is continuous with the cell layer covering the young pharynx (Plate II. Fig. 11). The cavity is at first closed on all sides, but eventually communicates with the common pharyngeal chamber. The lumen of the pharynx is formed by an infolding of its free end, which projects into the cavity. Although I have not been able to trace directly all the steps in the invagination, I have seen specimens where the lumen was lined throughout with an epithelium, and where there was as yet no connection with the intestine. The epithelium lining the lumen is continuous with that covering the outer surface of the young pharynx, and hence with that lining the pharyngeal cavity, and it presents the same histological conditions as the latter (Plate II. Fig. 11). Figure 14 represents a cross section of a young pharynx somewhat advanced in development, where the cellular structure of both the inner and outer epithelium is still evident; there are as yet no cilia, and no traces of the longitudinal muscles. I expect to describe in another paper the changes by which the mass of indifferent cells composing the young pharynx is converted into the ultimate histological structures of the mature pharynx.

The outer layer of the pharynx has never been described as possessing a distinctly cellular structure. Moseley ('74, p. 131), in speaking of land planarians, describes "an epithelium in which no definite cell structures could be observed; but it appeared transparent, and marked by vertical lines which might represent separation into cellular elements." Iijima ('84, p. 389) also saw "eine senkrechte Streifung." Lang ('81, p. 196, and '84, p. 109) speaks of it as a "cuticulaänliches Epithel" with flattened nuclei which it was difficult to see, and Minot ('77, p. 426) gives to it a well defined basement membrane. It is obvious from the description that I have given of the young pharynx that the outer layer, though ultimately much modified in appearance, is nevertheless an epithelial layer.

I could not demonstrate the presence of a cuticula with pore canals such as has been described by Iijima ('84, p. 390); neither could I discover anything answering to the nerve plexus described for other forms, nor could I detect any nerve tissue. From the automatic movements of the isolated pharynges, one would expect to find a complicated system of nerves, and perhaps one or more ganglionic centres.

In the mature pharynges the radial muscle fibres run from the outer to the inner epithelium, to both of which they are attached by their finely branched ends (Figs. 12 and 16). These muscles no doubt act antagonistically to the broad band of circular muscles in dilating the lumen of the pharynx, and by means of these two systems the peristaltic motions displayed by the pharynges are accomplished. Between the radial fibres there is a network of connective-tissue cells, and in the outer half of this middle zone occur the salivary ducts (Figs. 12 and 16, *dt. sal.*), which run the whole length of the pharynx and open at the edge of its lip. In the meshes of the connective-tissue network are seen fine granulations; these spaces are undoubtedly in communication with the pseudocœle of the body mesenchyma, and it is to the coagulation of the perivisceral fluid which has made its way out into the tissues of the pharynges that is due the granular appearance seen.

I have little to add to what has been written concerning the histology of the intestine, my observations agreeing in the main with those of Iijima. The structure is the same in the principal tracts and in the smaller branches; there are no differentiated gland cells. During the periods of most active digestion the intestinal cells are filled with highly refractive oil-like globules, of different sizes (Plate IV. Fig. 43), — the food matter absorbed by the cells. In this condition the cells are large, and protrude into the lumen, so that in the smaller branches of the intestine the latter has entirely disappeared. The contents of the cells are eventually absorbed by the neighboring tissues, and the intestinal cells themselves then appear vacuolated.

I have not been able to trace out the course of the *excretory canals*. Although I have endeavored many times to study them, I have never seen more than a few loops in the head region, and these were seen only when the animal was put under great pressure, resulting in disintegration of the tissues.

The *nervous system* of Phagocata agrees in the main with the descriptions given by Lang ('81, p. 53) and Iijima ('87, p. 349) for other planarians. The longitudinal nerve trunks unite near the anterior end of the body in a well developed brain mass (Plate III. Figs. 25 and 33), and posteriorly are connected with one another by fine commissures. Larger commissures unite the trunks to one another throughout their whole length, either running straight from trunk to trunk, or branching in their passage (Plate IV. Fig. 38). The latter condition may be regarded as closely related to one in which two commissures are united to each other by means of a connective, a condition that often occurs. There is no fixed relation between the number of transverse commissures and the lateral diverticulæ of the intestine, but lateral nerves are usually given off from the main stems at points opposite to the union of the latter with transverse commissures (Plate IV. Fig. 38). The main nerve trunks are prolonged anterior to the brain. They diminish rapidly in size, and give off several lateral branches, which are directed obliquely forwards and outwards (Plate III. Figs. 25 and 36), and they finally break up into minute branches which form a network. The lateral nerves from the main trunks run, sometimes with, sometimes without branching, to the margins, where they unite with a second pair of finer longitudinal nerves, — the marginal or peripheral nerves (Plate IV. Fig. 37, *n. pi'ph.*). The marginal nerves form the lateral edges of a great nervous network, which lies near the ventral surface just inside the sheet of longitudinal muscles. Figures 37 and 38 represent portions of two successive horizontal sections close to the ventral surface. The sections are 30 μ thick, and pass through the floor of the pharyngeal chamber; the light areas show where the knife has cut through the wall into the pharyngeal cavity. The animal having been sectioned from the ventral side, Figure 38 is the deeper (i. e. more dorsal) section. The position of the oral opening (*o*) indicates that the portions of the sections shown are from the same region of the body. In Figure 38 are seen the main nerve trunks (*n. l.'p.*) together with transverse commissures (*com. t.*) and lateral nerves (*n. l.*). It may be seen from Figure 37 how the median branches from the peripheral nerves (*n. pi'ph.*) break up into a network or plexus, which is distributed to the muscles (*plx. mu.*). This network covers the whole of the ventral surface, and at the extreme anterior end of the body is continuous with finer ramifications of the anterior longitudinal trunks. I could find no trace of a similar plexus in connection with the less developed muscles of the dorsal side.

The nervous system of planarians may be readily understood, it seems to me, if we regard it as composed of two more or less distinct parts, — a deep-seated and a more superficial portion. The deep-seated and more central part is present in all planarians hitherto investigated, and consists of the brain, longitudinal nerve trunks, their commissures, and the lateral nerves given off from them. The superficial portion consists of a nerve plexus which lies just underneath the longitudinal muscles, and may be confined to one or the other of the two surfaces, or may be wholly wanting. A conspicuous part of this superficial system, whenever it exists, is the marginal nerve. The connection between the deep and superficial portions of the nervous system is effected by means of vertical nerves running between the two, and, as I have found in Phagocata, the marginal nerve also serves in an indirect way the same purpose; for on the one hand it is connected with the lateral nerves of the central system, and on the other it forms the marginal terminus of the superficial system.

Lang ('81, p. 72) has described in Gunda a marginal nerve directly connected with the lateral nerves given off from the main trunks, but has been unable to find any other evidence of a plexus. In Rhynchodesmus, according to the same author ('81, p. 62), there are both dorsal and ventral plexuses, which are in contact with the deep surfaces of the longitudinal muscles, and are connected with the central system by vertical branches from the main trunks, from the lateral nerves, and from the transverse commissures, but there is no peripheral nerve. Lang ('81, p. 57) also finds a plexus in connection with the deeper longitudinal muscles in Planaria torva. Iijima ('84, p. 426) has likewise found a dorsal plexus in a similar position in Pl. polychroa and in D. lacteum, and Loman ('87, p. 76) has found the same conditions in Bipalium sumatrense and B. javanum. In Gunda ulvæ and Pl. abscissa there exists, according to Iijima ('87, p. 349), a second, dorsal pair of longitudinal stems, giving off branches that break up into a plexus and unite with the plexus from the lateral branches of the main trunks, the whole forming a "Nervenschlauch." He says that a "Randnerv" is present, but he does not state what are its relations to the plexuses.

From this brief survey it is obvious that Gunda represents one extreme, and Rhynchodesmus the other; since in the former there are no superficial plexuses, and in the latter there is a superficial plexus on both dorsal and ventral surfaces in addition to the parts found in Gunda, except that Rhynchodesmus has no marginal nerve. Both Phagocata and Planaria abscissa are intermediate between these extremes, Pl. abscissa possessing only the dorsal portion of the superficial system (in which a special dorsal longitudinal nerve has arisen), and Phagocata having only the ventral portion of that system. Both possess, however, the marginal nerve found in Gunda, and I believe that it probably sustains in Pl. abscissa the same relations to the deep portion of the nervous system that I have found to exist in Phagocata.

It is evident, I think, from what I have shown in Phagocata, that the marginal nerve is to be regarded as one of the means of communication between the central and superficial parts of the nervous system; or perhaps rather as a differentiation of that portion of the superficial system which is put in connection with the deep system by means of the lateral branches from the main trunks.

It may perhaps be reasonable to suppose that the more concentrated condition in Gunda has been brought about by a process of centralization from the more diffuse and more primitive (?) condition shown in Rhynchodesmus.

The brain is formed on the same plan as that of Gunda (Lang, '81, p. 67; '81^a, p. 213). I find two commissures, a larger anterior commissure which Lang calls in Gunda the sensory, and a smaller posterior one which he calls motor (Plate III. Figs. 23, 33, and Plate IV. Figs. 39, 46). The posterior commissure lies somewhat behind and below the anterior one. It directly connects the longitudinal nerve trunks, since it lies in the same ventral plane with them, while the anterior commissure, occupying a higher plane, is only indirectly united to these; viz. by means of the lateral masses of the brain from which vertical commissural fibres (the motor-sensory commissures of Lang) extend to the nerve trunks. Lang describes four pairs of nerves as arising from the lateral sensory masses of the brain. I cannot discover that there is any fixed number in Phagocata. The only well defined one is the optic nerve (Plate IV. Fig. 40, *n. opt.*). A great sheet of fine nerves is given off from the lateral surface of the brain, and, spreading out fan-like, runs forward to the anterior margin of the body (Plate III. Figs. 25 and 34, *n.*). It is from these nerves that the "Tastorgane" of this highly sensitive portion of the body receive their nerve supply.

A comparison of the figures will make clear the relation of the different parts of the brain. Figures 26 to 31 are from cross sections through the region of the brain taken at intervals of 60 μ. Figures 32 to 36 are consecutive sections in the horizontal plane, Figure 32 being the most dorsal of the series.

Lang ('81, p. 79) speaks of a "Zellenbeleg von wirklichen Ganglienzellen" around the brain of Triclads. Iijima ('87, p. 353) describes these cells as being unipolar with extremely delicate processes. I also find a layer of closely packed cells with large nuclei around the brain, more especially about the so called sensory portions (Plate III. Figs. 26–31, Plate IV. Figs. 39 and 40), but I cannot say that these are ganglionic cells. They resemble in every way connective-tissue cells; they react like them with stains, and are more prominent only on account of their compact arrangement. The nuclei of the two large "Substanzinseln" in the lateral masses of the brain (Plate III. Figs. 28, 33, Plate IV. Fig. 39, *con't. tis.*) are both identical and continuous with the nuclei surrounding the brain, and those found in the main nerve trunks cannot be distinguished from them. The ganglionic cells occurring *in* the nerve tissue are not as large, nor do their nuclei stain as deeply, as those occurring *around* the brain mass. I therefore believe that the latter belong to the mesenchyma, and that the "Substanzinseln" are only intrusive connective tissue.[1] Aside from this, I can add nothing to the observations of Iijima on the finer structure of the nervous tissue. The longitudinal nerve trunks in some places appear to be double for a considerable distance, being split, as it were, by the ingrowth of mesenchymatous tissue (Plate III. Figs. 33 to 36, and Plate IV. Fig. 38). All such openings, as pointed out by Lang ('81, p. 56), occur between the points of origin of the lateral nerves.

The *testes* are numerous, and are found lying close together throughout the whole length of the animal. Their development takes place before that of the yolk glands. While the latter are still in an early stage of development, spermatogenesis has been completed, the testes have disappeared, and the spermatozoa are found filling the vasa deferentia. The testes first appear as spherical clusters of cells, which by division increase in number and arrange themselves in the form of hollow spheres. Some of the peripheral cells divide rapidly into small spherical cells, that come to lie in the cavity of the testis. These cells become elongated or pear-shaped, and are then differentiated into two portions, a deeply stainable thickened end, and a tapering tail portion (Plate II. Fig. 24). Further elongation takes place, until the form of the adult spermatozoön is reached. Many stages of development can be seen in the same testis. The different stages occur in distinct groups, each group probably being the product of one of the parent cells. The wall of the testis, when the spermatozoa first begin to develop, is composed of many cells, most of which by division go to form spermatozoa; a few of the cells, however, are differentiated into flattened epithelium, which constitutes the wall of the capsular testis (Plate II. Fig. 24, *e'th.*).

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[1] Since I came to these conclusions in regard to the mesenchymatous character of the so called "Substanzinseln," I have been gratified to learn that my conclusions agree with those of Loman ('87, p. 77). In Bipalium, then, as well as in Phagocata, the "Substanzinseln" present in all particulars the same differences from ganglionic cells.

I have not succeeded in ascertaining the exact manner in which the spermatozoa find their way into the vasa deferentia, but Iijima's statement ('84, p. 408) that they do not wander through the spaces of the mesenchyma is certainly incorrect. The testes give rise to tubular prolongations, but whether these are directly connected with the vas deferens or first unite into one or more vasa efferentia, I cannot say. The testicular canals appear to be direct outgrowths of the wall of the testis. Their walls and those of the vasa deferentia have the same simple structure (compare Plate II. Figs. 23 and 24), being composed of a single layer of thin epithelium. The nuclei in the walls of the tubes often occur in pairs, and thus suggest that the cells to which they belong have recently undergone division (Fig. 24).

According to Moseley ('74, p. 139), the testes in land planarians open directly into the vasa deferentia; Minot ('77, p. 432), on the contrary, speaks of fine testicular canals that unite to form larger tubes. Kennel ('79, p. 137) states that the testes, arranged in rows, fuse to form the vasa deferentia.

The anterior ends of the vasa deferentia in Phagocata lie on either side of the pharyngeal chamber in the region of the mouth opening. They have the form of large elongated sacs (Plate IV. Fig. 42, *x*) which open into comparatively narrow tubes (*va. df.*), which are of an even calibre, and much convoluted and twisted. They run backward parallel to each other until near the base of the penis; they then turn at right angles toward the middle plane, where they unite to form a single tube which terminates at the apex of the penis. The spermatozoa when ripe leave the testes by the testicular canals previously described, and pass into the vasa deferentia, which become filled from their enlarged blind ends up to a point beyond that where they unite to enter the penis. Here the spermatozoa remain stored until arranged into spermatophores, in which form they pass into the vagina of another individual. After the spermatozoa have found their way to the vasa deferentia, all traces of the testes disappear.

Physiologically considered, the vasa deferentia of Triclads are to be considered as vesiculæ seminales. In Polyclads and in Rhabdocœles a vesicula seminalis is present. This organ has been described for land planarians by Moseley ('77, p. 278) and Loman ('87, p. 81), and Kennel ('88, p. 460) speaks of "mehrfach gewundenen Samenblasen" in Planaria alpina. There can be no doubt that the terminal enlargements found in Phagocata are a provision for the storage of a great number of spermatozoa, as their size is found to vary in different individuals and on different sides of the same individual according as the number of spermatozoa is large or small.

The *penis* or intromittent organ is a highly muscular plug-like structure (Plate IV. Fig. 42, *pe.*) that lies in the genital atrium or penis sheath. It is covered with a flattened epithelium, under which there are alternating layers of circular and longitudinal muscles, five of each, forming a thick zone. Immediately outside the epithelial lining of the tube there is a band of circular muscles, and between these and the outer muscles there is a broad zone occupied by a meshwork of muscular fibres, prominent among which are those having a radial direction. The lumen of the penis is not of an even calibre, but consists of a succession of chambers, or dilatations, lined with a granular epithelium, which is probably glandular. It is within the lumen of the penis, no doubt, that the spermatophores are formed. The sheath of the penis is lined with an epithelium of cylindrical cells, the nuclei of which lie close to the bases of the cells, and are stained deeply, while the glandular cell substance is stained only slightly. These cells also may be glandular, but if so, I can find no explanation for their faint reaction with staining reagents. In that respect they differ from all other glandular tissue.

The female sexual organs consist of a pair of ovaries with their oviducts, the vitellarium or yolk gland, the uterus, and the vagina. The single pair of *ovaries* is situated in the anterior part of the body a little behind the brain mass. They are symmetrically placed on the ventral side of the body just dorsad of the main nerve trunks, one on either side. They appear as rounded sacs filled with ova (Plate II. Fig. 21). The wall of the ovary is a delicate membrane, in which I could detect no sign of cell structure, such as Moseley ('74, p. 137) found in the ovary of land planarians. Scattered in between the ova are the nuclei of a connective-tissue network that fills the spaces between the ova (Plate II. Fig. 21, *nl. con't. tis.*). Iijima ('84, p. 412) considers the branching cells between the ova as rudimentary egg cells, at whose expense the ova develop. I have not yet seen different stages in the development of the ova.

Intimately associated with the ovaries are two prominent compact cell masses with deeply stained nuclei, which may provisionally be called *parovaria* (Plate II. Fig. 21, *vt'm.*). They are larger than the ovaries, and envelop them above, in front, and on the outside; that is to say, the ovaries are surrounded on three sides, being partially imbedded, so to speak, in these cell masses. The latter are present in every individual, and their size relative to that of the ovaries varies only with the condition of the sexual organs. They are smallest during the development of the spermatozoa, and are most prominent at the time when the yolk glands have reached their full development. For a long time these cell masses puzzled me. I believed them to correspond to the second pair of rudimentary ovaries described by Iijima ('84, p. 412) for Polycelis tenuis, and I at first accepted his interpretation of their significance; but sections through additional material, where the female organs were not so advanced, served to show their true meaning; *they are the organs which give rise to the yolk glands.* At an early stage in the development of the testes no yolk glands are present, but they begin to appear at the time when the spermatozoa are ripening.

The first traces of the *yolk glands* are seen in branching chains of cells, which arise as outgrowths from the parovaria. Each cell has a large nucleus that is stained deeply in carmine. In these chains the cells lie either in a single row, or it may be in several rows (Plate II. Figs. 19 and 19*a*). The nuclei are large and granular, and occupy the greater part of the cell. It is to be inferred that the cells are dividing rapidly, since nuclei are found in all stages of division, and two nuclei are frequently seen in the same cell; the division appears to be direct, or amitotic (Plate II. Figs. 19 and 22). The rudimentary yolk glands occupy at first the ventral regions around the oviducts, but afterwards they send branches from there dorsad, until there is formed a dendritic system of rapidly dividing cells, which ramify through the tissues. From each of the cell masses around the ovaries is derived one half of the yolk system, that belonging to its own side of the body. The cell chains of the young yolk glands are seen to be directly connected with the parovarial cell masses, and histologically the structure of the two is identical (compare Fig. 19 with Fig. 22, Plate II.). Furthermore, at the time of development of the yolk glands there is a very active division of the cells of the parovarial masses, a condition that does not exist when the yolk glands have matured. A similarity in the condition of the cells of the yolk glands and those of the parovarial masses is evident at all stages of development. The young cells of the yolk glands increase in size, but do not grow as rapidly as the surrounding protoplasm, and therefore the nucleus becomes smaller in proportion to the size of the cells. Many highly refractive granules appear in the protoplasm, and increase in number with the growth of the cells, till eventually, when the cells have attained their full size, they form a relatively large proportion of the cell mass (Plate IV. Fig. 45). Corresponding to the changes that take place in the yolk cells, there is a slight increase in the size of the parovarial cells, in which there is also an accumulation of highly refractive granules (Plate IV. Fig. 44), but the nuclei retain more nearly their original proportions to the cells than in the case of the yolk cells. In addition to the identity of histological structure, a most striking evidence of the derivation of the yolk glands from the parovarial cell masses is found in the reaction of both kinds of cells with staining fluids, more especially with picrocarminate of lithium. Figures 44 and 45, Plate IV., represent respectively sections through parovarial cells and mature yolk-gland cells of the same individual. Figures 19 and 22, Plate II., are sections from another individual; Figure 22 is a section of young parovarial cells, and Figure 19 of incipient yolk-gland cells. Upon comparison of Figures 19 and 22 with Figures 45 and 44, it will be noticed that, in addition to the appearance of the granules in the protoplasm of the older cells, there has been an increase in the size both of the yolk cells and of the cells of the parovarium. It is my belief, then, that the two large dendritic yolk glands arise by cell proliferation from the parovarial organs which exist in intimate relation with the ovaries.

Iijima ('84, p. 412) describes a pair of structures lying in front of the ovaries in Polycelis tenuis as being composed of a solid mass of cells, and as resembling young ovaries, so that this species possesses, in his opinion, two pairs of ovaries, one of which is rudimentary. On account of their terminal position, he considers these rudimentary structures, although not the functional ovaries, as the homologues of the single pair of ovaries present in other species. His account of the growth of the yolk glands, as given at p. 417, coincides with my observations, but concerning the source of the chains of young yolk cells he says (p. 455): "Wir dürfen sagen, dass die Dotterstränge durch Vermehrung einzelner Zellen, welche in dem Mesenchym sich befinden, ihren Ursprung nehmen." But his evidence that the "Dotterstränge" arise *in situ* is not satisfactory. It is to be regretted that he has not given a fuller account of the so called rudimentary ovaries of Polycelis, which, I am almost certain, are the equivalents of the parovarial cell masses of Phagocata.

The absence of yolk glands in Moseley's land planarians can be accounted for by assuming that in his material they were not yet ripe, as was probably the case. He states ('74, p. 137), however, that there is occasionally present in Bipalium, "just externally to the lower extremities of the ovaries, a small mass of large nucleated cells connected by a pedicle with the ovary itself." He considers that "it may represent a yolk-gland in a rudimentary condition." With this I fully agree, and further believe that this rudimentary yolk gland is the homologue of the structure which in Phagocata I have called parovarium.

The presence of a vitellogenous organ in Phagocata, together with the condition found in Polycelis by Iijima and in Bipalium by Moseley, suggests a discussion of the relations of the ovaries and vitellaria. Yolk glands have long been considered as resulting from the differentiation of the ovaries. Gegenbaur, as stated in his text-book ('70, p. 281), considers the yolk glands to be "Theile eines ansehnliches Ovars." Hallez ('79, p. 63) maintains that "le *vitellogène* n'est autre chose qu'une partie différenciée de l'ovaire," and according to Lang ('81^a, p. 228), "Die Keimstöcke und Dotterstöcke der Tricladen sind einander gleichwerthig. Sie entstehen aus Zellen, die anfangs nicht von einander unterscheiden lassen." Among Rhabdocœles all gradations are found, from an undifferentiated "Keimdotterstock," where ova and yolk cells are developed in different portions of the same organ, to conditions in which the ova and yolk cells are produced in distinct and separate organs. The yolk glands, then, have arisen by a divison of labor from a simple germ gland, as has already been formulated by Graff ('82, p. 130) in the following words: "Die Keimdotterstöcke müssen wir uns aus Ovarien durch einfache Arbeitstheilung hervorgegangen denken; durch räumliche Trennung der verschieden functionirenden Abschnitte des Keimdotterstockes entstanden schlieslich die Keim- und Dotterstöcke." I consider the condition found in Phagocata to be less differentiated than that exhibited by Pl. tenuis (Iijima), inasmuch as the cells which form it still retain a more intimate relation to the true ovary than they do in the latter case.

The union of the yolk glands with the oviducts is a secondary one; it takes place at intervals throughout their length. I have not studied this in detail, but, as far as I have learned, the conditions agree with the careful description given by Iijima ('84, p. 415). The oviducts open into the vagina just above the point where it enters the genital atrium (Plate IV. Fig. 42).

The *uterus* (Plate IV. Fig. 42, *ut.*) is a sac-like organ lying just anterior to the penis, and has thick walls that are thrown into many folds. It is lined with an epithelium of elongated cylindrical or pyriform cells of a glandular nature. The appearance of the cells varies with the activity of their secretion; the protoplasm may be either homogeneous, or filled with oil-like globules, or it may be vacuolated. The cells rest upon a fine basement membrane. There is no musculature, and there are no cilia.

The mouth of the uterus is prolonged into a tube with thick muscular walls, *the vagina* (Plate IV. Fig. 42, *vag.*), which runs backward, passing above and to the left of the penis and then dipping down toward the ventral side of the body, where it opens into the genital atrium. Where the vagina arises from the uterus it is lined with a ciliated epithelium of low cubical cells, and possesses a musculature of circular and longitudinal fibres. As it passes backward, the cells of the lining epithelium become taller and cylindrical (Plate II. Fig. 15, *e'th.*), and the nuclei are elongated. The outer ends of the cells show distinct granulations, and the contour of the lumen becomes uneven; the glandular nature of the cells now becomes apparent. Along with the change in the appearance of the cells of the lining epithelium there is an increase in the thickness of the musculature, which now consists of alternating layers of circular and longitudinal fibres. The musculature of the vagina reaches its greatest development at the point where it bends toward the ventral side of the body; from this point onward the cells lose their glandular character, and the musculature diminishes in thickness, till, at the point where the vagina receives the oviducts, it again consists of only a single layer each of circular and longitudinal fibres. Moseley ('74, p. 141) and Iijima ('84, p. 420) speak of radial fibres in the walls of the vagina; but I could not find any.

The accessory female organs of Triclads have been the subject of much discussion. There are no other structures about which so many opinions at variance with each other have been advanced. The organ which I have called the uterus is regarded by Iijima ('84, p. 419) as a simple gland whose secretions go to form the cocoon. In his opinion, it has no function in connection with the union of the sexual elements; he considers it homologous with the shell gland of Cestodes and Trematodes. According to Kennel ('88, p. 458), it is to be considered as a receptaculum seminis, and its secretions serve to preserve the spermatozoa. Hallez ('87, p. 24) maintains that fecundation takes place in the uterus, and that in it the yolk cells join the egg cells. According to Hallez, there is a division of labor among the cells lining the uterus. The majority of them secrete the substance of the cocoon, others secrete "un liquide spécial" to support the vitality of the male elements, and possibly to aid in fecundation. He states that in Pl. polychroa the cocoon is produced in the uterus, but as regards Dendrocœlum lacteum he agrees with Iijima in maintaining that the cocoon is formed in the genital cloaca or atrium. In Phagocata I have found ova as well as spermatozoa in the uterus, and believe that fecundation takes place there. The spermatophores are deposited in the vagina and from there the spermatozoa make their way into the uterus. I believe also that a portion of the contents of the cocoon are secreted by the uterus, but that the substance of its wall, the shell, is produced from the glandular lining of the vagina, so that in Phagocata at least the "uterus" cannot be regarded as homologous with the shell gland of Cestodes. It is my purpose to discuss at length these questions, together with that of the formation of the spermatophore, in a subsequent paper on the embryology of this species.

No organ comparable with the "muskulösen Drüsenorgan" of Iijima ('84, p. 422), or the "vésicule (bourse) copulatrice" of Hallez ('79, p. 57, and '87, p. 20), is present.

Summary.

Phagocata differs from all known Triclads in possessing, besides a pharnyx which opens into the intestine at the junction of its three main trunks, many additional pharynges which are joined to the two lateral trunks of the intestine. The lateral pharynges are histologically identical with the median one; they differ from the latter only in size; the more remote they are from it, the smaller they are.

The rhabditi or dermal rods lie between the cells of the hypodermis, not in them. They are developed in cells lying in the sub-hypodermal mesenchyma; the cells are connected with the hypodermis by fine tubular prolongations. The connection of the parent cells of the rhabditi with the exterior is a primitive one, and the rods enter the hypodermis by emergence along these prolongations. The rhabditi are ultimately discharged from the hypodermis, and new ones are constantly being developed in new parent cells. They are slowly soluble in water, and are used for securing prey and for protection.

The parent cells of the rhabditi are unicellular glands, and the rods are their condensed secretions.

The "Stäbchenstrassen" of Rhabdocœles are homologous with the slime glands in Phagocata.

The basement membrane is a product of the hypodermis. It is structureless.

The pigment is intercellular, occurring in the form of scattered granules.

The pseudocœlar spaces of the mesenchyma are intercellular in origin, and sagittal muscles are directly continuous with processes of the mesenchyma cells.

The nervous system consists of a deeper and a superficial portion; a marginal nerve indirectly connects the two. The condition in Phagocata may be intermediate between that of Gunda and Rhynchodesmus.

The brain presents two commissures, an anterior and a posterior one, uniting the longitudinal nerve trunks. The so called "Substanzinseln" are intrusive connective tissue.

The testes give rise to tubular outgrowths, the vasa efferentia. The vasa deferentia have terminal enlargements and function as vesiculæ seminales.

The yolk glands arise by cell proliferation from two cell masses, the parovaria, which are in immediate contact with the ovaries. The intimate connection of the parovaria with the ovaries indicates the differentiation of the ovary and vitellarium from a common gland.

The so called uterus is not only a gland; it is a place in which the sexual elements are brought together, and where fertilization consequently takes place.

Cambridge, August, 1890.

It was not until this paper had gone to press that I had access to the recent work of Böhmig ('91) on Rhabdocœles. It was then too late for any detailed review. I am gratified to observe, however, that he has arrived at conclusions from his studies of Rhabdocœles which agree in many points with those which I have expressed in the foregoing paper, especially in his statements as to the fate and significance of rhabditi.

BIBLIOGRAPHY.

Böhmig, L.

'86. Untersuchungen über rhabdocöle Turbellarien. I. Das Genus Graffilla v. Jhering. Arbeiten a. d. zoolog. Inst. z. Graz, Bd. I. No. 1, 1886. Also in Zeitschr. f. wiss. Zool., Bd. XXXIV. Heft 2, pp. 291–328, Taf. XI., XII. 14 May, 1886.

'90. Untersuchungen über rhabdocöle Turbellarien. II. Plagiostomum und Cylindrostomina Graff. Zeitschr. f. wiss. Zool., Bd. LI. Heft 2, 3, pp. 160–479, Taf. XII.–XXI. 31 Dec., 1890.

Braun, M.

'81. Beiträge zur Kenntniss der Fauna baltica. I. Ueber Dorpater Brunnenplanarien. Arch. f. d. Naturk. Liv-, Ehst- und Kurlands, [2.] Bd. IX. Lief. 4, pp. 289–341, 1 Taf. Dorpat, 1881.

Diesing, K. M.

'87. Systema Helminthum. Vindobonæ apud Wilhelmum Braunmüller. Vol. I., xiii + 379 pp. 1850.

'62. Revision der Turbellarien. Abtheilung: Dendrocoelen. Sitzungsb. d. k. Akad. Wien, math.-naturw. Cl., Bd. XLIV. Abth. I., 1861, pp. 485–578. 1862.

Eisig, H.

'87. Monographie der Capitelliden des Golfes von Neapel und der angrenzenden Meeresabschnittes. Fauna und Flora d. Golfes v. Neapel, XVI. xxvi + 906 pp., 20 Holzschn., 37 Taf. 1887.

Gegenbaur, C.

'70. Grundzüge der vergleichenden Anatomie. Zweite Aufl. Leipzig, 1870.

Girard, C.

'51. A brief Account of the Fresh-water Planariæ of the United States. Proc. Boston Soc. Nat. Hist., Vol. III. 1848–1851, pp. 264, 265. Presented 20 March, 1850. Cambridge, 1851.

51. Die Planarien und Nemertinen Nord-Amerika's. Nord-amerik. Monatsb. f. Natur- u. Heilkunde, Bd. II. No. 1, p. 1. Philadelphia, January, 1851.

Graff, L.

'74. Zur Kenntniss der Turbellarien. Zeitschr. f. wiss. Zool., Bd. XXIV. Heft. 2, pp. 123–160, Taf. XIV.–XIX. 13 April, 1874.

'82. Monographie der Turbellarien. I. Rhabdocoelida. Leipzig, Engelmann, 1882. xii + 441 pp., 12 Holzschn., Atlas, 20 Taf., fol.

Haldemann, S. S.

'40. Supplement to Number One of "A Monograph of the Limniades, or

Freshwater Univalve Shells of North America," containing Descriptions of apparently new Animals in different Classes, etc. 3 pp. Philadelphia, October 18, 1840.

Hallez, P.

'79. Contributions à l'histoire naturelle des Turbellariés. Travaux d. l'Instit. zool. d. Lille, Fasc. II., viii + 213 pp., 9 pl. 1879.

'87. Embryogénie des Dendrocœles d'eau douce. Paris, Octave Doin, 1887. 107 pp., 15 photogravures, 5 pl., 8vo.

Hamann, O.

'85. Beiträge zur Histologie der Echinodermen. Heft 2. Die Asteriden anatomisch und histologisch untersucht. Jena, Fischer, 1885. iv + 125 pp., 3 Holzschn., 7 Taf., 8vo.

Hertwig, O. and R.

'81. Die Coelomtheorie. Versuch einer Erklärung des mittleren Keimblattes. Jenaische Zeitschr., Bd. XV. Heft 1, pp. 1–150, Taf. I.–III. 25 Jan., 1881.

Iijima, Isao.

'84. Untersuchungen über den Bau und die Entwicklungsgeschichte der Süsswasser-Dendrocoelen (Tricladen). Zeitschr. f. wiss. Zool., Bd. XL. Heft. 3, pp. 359–464, Taf. XX.–XXIII. 27 June, 1884.

'87. Ueber einige Tricladen Europa's. Jour. College of Science Imp. Univ. Japan, Vol. I. pp. 337–358, Pl. XXV. Tokyo, 1887.

Jensen, O. S.

'78. Turbellaria ad Litora Norvegiæ occidentalia. Turbellarier ved Norges Vestkyst. Bergen, J. W. Eides, 1878. vi + 97 pp., 8 pl., fol.

Jhering, H. von.

'80. Graffilla muricicola, eine parasitische Rhabdocoele. Zeitschr. f. wiss. Zool., Bd. XXXIV. Heft 1, pp. 147–174, Taf. VII. 1 March, 1880.

Keferstein, W.

'89. Beiträge zur Anatomie und Entwicklungsgeschichte einiger Seeplanarien von St. Malo. Abhandl. d. k. Gesellsch. d. Wissensch. z. Göttingen, Bd. XIV. pp. 3–38, Taf. I.–III. 1869.

Kennel, J.

'79. Die in Deutschland gefundenen Landplanarien Rhynchodemus terrestris O. F. Müller und Geodesmus bilineatus Mecznikoff. Arbeit. a. d. zool.-zoot. Inst. Würzburg, Bd. V. Heft 2, pp. 120–159, Taf. VII. 15 Dec., 1879.

'88. Untersuchungen an neuen Turbellarien. Zool. Jahrbücher, Abth. f. Anat. u. Ontog. d. Thiere, Bd. III. Heft 3, pp. 447–486, Taf. XVIII., XIX. 30 Nov., 1888.

Lang, A.

'80. Notiz über einen neuen Parasiten der Tethys aus der Abtheilung der rhabdocoelen Turbellarien. Mittheil. a. d. zool. Stat. z. Neapel, Bd. II. Heft 1, pp. 107–112, Taf. VII. 1880.

'81. Untersuchungen zur vergleichenden Anatomie und Histologie des Nervensystems der Plathelminthen. IV. Das Nervensystem der Tricladen. V. Vergleichende Anatomie des Nervensystems der Plathelminthen. Mittheil. a. d. zool. Stat. z. Neapel, Bd. III. Heft 1, 2, pp. 53–95, Taf. V., VI. 2 Dec., 1881.

'81^a. Der Bau von Gunda segmentata und die Verwandtschaft der Plathelminthen mit Coelenteraten und Hirudineen. Mittheil. a. d. zool. Stat. z. Neapel, Bd. III. Heft 1, 2, pp. 187–250, Taf. XII., XIII. 9 Dec., 1881.

'84. Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrezenden Meeresabschnitte. Eine Monographie. Fauna u. Flora d. Golfes v. Neapel, XI., ix + 688 pp., 54 Holzschn., Atlas 39 Taf. Leipzig, 1884.

Leidy, J.

'48. Description and Anatomy of a new and curious Sub-genus of Planaria. Proc. Acad. Nat. Sci. Philadelphia, Vol. III. 1846–1847, pp. 248–251. 1848. Presented 31 Aug., 1847.

'85. Planarians. The Museum, Vol. I. No. 4, pp. 49–52, 1 woodcut. Philadelphia, Aug., 1885.

Lippitsch, K.

'89. Beiträge zur Anatomie des Derostoma unipunctatum Oe. Arbeit. a. d. zool. Inst. z. Graz, Bd. II. No. 6, 1889. Also in Zeitschr. f. wiss. Zool., Bd. XLIX. Heft 1, pp. 325–345, Taf. VIII. 13 Dec., 1889.

Loman, J. C. C.

'87. Ueber den Bau von Bipalium, Stimpson, nebst Beschreibung neuer Arten aus dem indischen Archipel. Bijdragen tot de Dierkunde. Uitgegeven d. h. Genootschap Natura Artis Magistra, te Amsterdam. Afl. 14, pp. 63–88, Pl. I., II. 1887.

Mecznikow, El.

'66. Ueber Geodesmus bilineatus Nob. (Fasciola terrestris O. Fr. Müller?), eine europaische Landplanarie. Bull. d. l'Acad. Imp. d. Sci. d. St. Pétersbourg, Tom. IX. No. 4, pp. 433–447, 1 pl. 28 Feb., 1866. Also in Mélanges Biologiques, Tom. V. pp. 544–565, 1 pl. 1865.

Minot, C. S.

'77. Studien an Turbellarien. Beiträge zur Kenntniss der Plathelminthen. Arbeit. a. d. zool.-zoot. Inst. Würzburg, Bd. III. Heft 3, pp. 405–471, Taf. XVI.–XX. 20 Feb., 1877.

Moseley, H. N.

'74. On the Anatomy and Histology of the Land-Planarians of Ceylon, with some Account of their Habits, and a Description of two new Species, and with Notes on the Anatomy of some European Aquatic Species. Philos. Trans. Roy. Soc. London, Vol. CLXIV. pp. 105–171, Pl. X.–XV. 1874.

'77. Notes on the Structure of several Forms of Land Planarians, with a Description of two new Genera and several new Species, and a List of all the Species at present known. Quart. Jour. Micr. Sci., Vol. XVII. N. S., No. 67, pp. 273–292, Pl. XX. July, 1887.

Schmidt, E. O.

'48. Die rhabdocoelen Strudelwürmer (Turbellaria rhabdocoela) des süssen Wassers. Jena, Fr. Mauke, 1848. 65 pp. 6 Taf., 8vo.

Schneider, Anton.

'73. Untersuchungen über Plathelminthen. Vierzehnter Bericht d. Oberhessischen Gesellsch. f. Natur- u. Heilkunde, pp. 69–140, Taf. III.–VII. Giessen, 1873.

Schneider, Camillo.

'90. Histologie von Hydra fusca mit besonderer Berücksichtigung des Nervensystems der Hydropolypen. Arch. f. mikr. Anat., Bd. XXXV. Heft 3, pp. 321–379, Taf. XVII.–XIX. 9 June, 1890.

Siebold, Th. von.

'50. Bericht über die Leistungen in der Naturgeschichte der Würmer, Zoophyten und Protozoen während der Jahre 1845, 1846 und 1847. Arch. f. Naturg., Jahrg. XVI. Bd. II. pp. 351–468. 1850.

Stimpson, W.

'58. Prodromus Descriptioni Animalium Evertebratorum quæ in Expeditione ad Oceanum Pacificum Septentrionalem a Republica Federata missa, Johanne Rodgers Duce, observavit et descripsit. Pars I. Turbellaria Dendrocœla. Proc. Acad. Nat. Sci. Philadelphia, Vol. IX., 1857, pp. 19–31. 1858. Presented 24 Feb., 1857.

Vejdovsky, F.

'90. Note sur une nouvelle Planaire terrestre (Microplane humicola nov. gen., nov. sp.) suivi d'une liste des Dendrocœles observées jusqu'a présent en Bohême. Revue Biolog. d. Nord d. l. France, Ann. 2, No. 4, pp. 129–148, Pl. II., III. 1 Jan., 1890.

EXPLANATION OF FIGURES.

All the figures are from camera drawings of Phagocata gracilis, Leidy.

ABBREVIATIONS.

atr.	Genital atrium.
cil.	Cilia.
cl. rhb.	Parent cells of the rhabditi.
cl. sp'z.	Parent cells of the spermatozoa.
com. a.	Anterior commissure of the brain.
com. p.	Posterior commissure of the brain.
com. t.	Transverse commissure.
con't. tis.	Connective tissue.
dt. sal.	Salivary duct.
e'th.	Epithelium.
e'th. ex.	External epithelium.
e'th. i.	Internal epithelium.
e'th. phy.	Epithelium of pharynx.
go'po.	Gonopore.
h'drm.	Hypodermis.
h'drm.'	Aborted cells of hypodermis.
in.	Intestine.
mb. ba.	Basement membrane.
ms'chy.	Mesenchyma.
mu. crc.	Circular muscles.
mu. crc. ex.	External circular muscles.
mu. crc. i.	Internal circular muscles.
mu. l.	Longitudinal muscles.
mu. l. ex.	External longitudinal muscles.
mu. l. i.	Internal longitudinal muscles.
mu. r.	Radial muscles.
mu. sag.	Sagittal muscles.
n.	Sensory nerve.
n. l.	Lateral nerve.
n. l.'a.	Anterior longitudinal nerve.
nl. con't. tis.	Nucleus of connective tissue.
nl. e'th.	Nucleus of epithelium.
n. l.'p.	Posterior longitudinal nerve.
nl. rhb.	Nucleus of parent cells of the rhabditi.
n. opt.	Optic nerve.
n. pi'ph.	Peripheral (marginal) nerve.
o.	Mouth opening.
oc.	Eye.
ov'dt.	Oviduct.
pe.	Penis.
phy. m.	Median pharynx.
phy. l.	Lateral pharynx.
plx. mu.	Nerves to muscular plexus.
rhb.	Rhabditi.
sec.	Secretions which do not form rhabditi.
sp'z.	Spermatozoa.
trn. i. a.	Anterior trunk of intestine.
trn. i. l.	Lateral trunk of intestine.
ut.	Uterus.
va. df.	Vasa deferentia.
vag.	Vagina.
vt'm.	Parovarium (vitellarium).
x.	Enlarged ends of vasa deferentia.

PLATE I.

Fig. 1. Portion of a longitudinal section of the dorsal wall of the body, showing the parent cells of the rhabditi and the position of the rhabditi in the hypodermis. × 900.

" 2. Cross section near the lateral margin of the dorsal side, in a region where there were no rhabditi, showing the hypodermis in its primitive condition. × 900.

In Figures 1 and 2 the basement membrane did not take the stain.

" 3. Longitudinal section through a region where there were many rhabditi which have been removed by partial maceration, showing the modified condition of the hypodermal cells due to the crowding of the rhabditi. × 900.

" 4. Longitudinal section of ventral wall of body, showing a young parent cell of the rhabditi, the nucleus almost filling the cell. The hypodermis removed. × 900.

" 5. Two parent cells of the rhabditi, from macerated material. × 960.

" 6. Longitudinal section of ventral wall showing two stages in the development of the parent cells of the rhabditi. Two small rhabditi have already been secreted in the larger cell. The hypodermis removed. × 900.

" 7. Stage in the development of the parent cells of the rhabditi next older than that shown in Figure 4. The cell has sunk deeper into the tissues, and the nucleus is smaller in relation to the size of the cell. Ventral wall of body, the hypodermis being removed. × 900.

" 8. Longitudinal section of ventral wall showing one of the rhabditi in the act of passing through the basement membrane. The hypodermis removed. × 900.

" 9. Showing the appearance of the rhabditi after having been acted upon by picric acid. × 900.

" 10. Longitudinal section of the ventral wall showing one of the parent cells of the rhabditi filled with the rods. The remnants of another cell represented by the nucleus and three rhabditi are seen close by. The hypodermis has been removed. × 900.

Owing to a mistake of the lithographer, the nuclei of the parent cell (*nl. rhb.*) in Figure 10 are not represented as being granular, as they should be.

Woodworth Phagocata

PLATE II.

Fig. 11. Cross section of an individual in the region of a young budding pharynx. Its connection with the intestine has not yet been established. × 300.

" 12. Portion of a cross section through one of the lateral pharynges. × 320.

" 13. A worm feeding on an Annelid; five of the pharynges are visible. Killed with hot corrosive sublimate while feeding. × 10.

" 14. Portion of a cross section through young pharynx, showing the nucleated epithelia. The other tissues are not yet differentiated. × 300.

" 15. Portion of a cross section through the vagina in the region where the musculature reaches its greatest development. × 120.

" 16. Longitudinal section of the wall of one of the smaller pharynges. × 500.

" 17. Portion of a longitudinal section through the slime glands in the head region, where they pass over the brain. × 300.

" 18. Portion of a cross section of the body to show the reticulated mesenchyma and its relation to sagittal muscles. × 500.

" 19 and 19*a*. Portions of the incipient yolk glands; in Figure 19 the nuclei are seen in process of division. × 820.

" 20. A partial reconstruction of the whole worm showing the pharynges and their relation to the intestinal tract. × about 20.

" 20*a*. Outline to show the appearance of the living worm while in progression. × 9.

" 20*b* and 20*c*. Outlines showing forms assumed by the worm when at rest. × 6.

" 21. Longitudinal section through the ovary and parovarium showing their relation to each other. × 300.

" 22. Section through a parovarium at the time when the yolk glands are beginning to develop. From the same individual as Figures 19 and 19*a*. × 820.

" 23. Cross section through the vas deferens. × 300.

" 24. Portion of a section which passes through one of the testicular sacs, showing its tubular outgrowth, — vas efferens × 300.

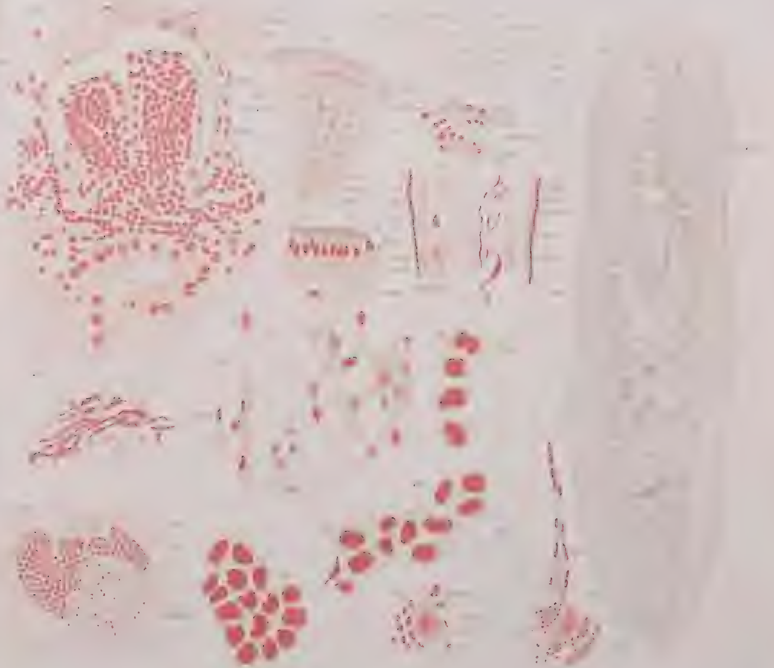

PLATE III.

Fig. 25. Horizontal section through the head region showing the brain and sensory nerves, and the relation of the anterior longitudinal nerve to the marginal nerve (*n. pi'ph.*). The right-hand side of the section is a little more dorsal than the left. × 52.

" 26–31. From a series of cross sections through the brain region. The sections are taken at intervals of $60\,\mu$. Figure 26 is the most anterior. × 52.

" 32–36. From a series of horizontal sections through the brain region, cut from the dorsal side. The sections are consecutive, and $30\,\mu$ in thickness. × 52.

PLATE IV.

Figs. 37 and 38 Two consecutive horizontal sections (30μ in thickness) from the ventral side passing through the floor of the pharyngeal chamber. Figure 37 is the more ventral, and shows the marginal nerve; the relation of the latter to the longitudinal trunks is evident upon comparing Figures 37 and 38. × 27.

" 39 and 40. Two longitudinal sections, parallel with the sagittal plane, through the brain region. × 52.

" 41. From an isolation preparation, showing one of the sub-hypodermal glands from the region of the gonopore. × 700.

" 42. A view of the sexual organs showing their relations to one another. The figure was accidentally inverted by the lithographer, thus bringing the posterior end uppermost. Partially diagrammatic. × 35.

" 43. Portion of a cross section of one of the lateral branches of the intestine. × 450.

" 44. Portion of a section through a parovarium of an individual in which the yolk glands were fully developed. × 680.

" 45. Section through a portion of a yolk gland from the same individual as Fig. 44. × 260.

" 46. Sagittal section through the brain, showing the two commissures. × 60.

" 47. Portion of a tangential section of one of the pharynges, to show the cell boundaries of the external epithelium. From an isolated pharynx killed in hot silver nitrate. × 350.

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No. 2. — *The Compound Eyes in Crustaceans.* By G. H. Parker.[1]

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INTRODUCTION.

Some four years ago, at the suggestion of my instructor, Dr. E. L. Mark, I began the investigation of the compound eyes in Crustaceans. In order to familiarize myself with the subject, I determined to study at first in detail the structure of the eyes in a single species, and for this purpose I turned my attention to our common lobster, Homarus americanus. My results were published in a paper entitled "The Histology and Development of the Eye in the Lobster." Since the publication of that paper, I have had the opportunity of examining the eyes in a number of other Crustaceans, and my observations and conclusions concerning these eyes are contained in the following pages.

The *material* which I have used in the present study was in part supplied to me through the kindness of several friends, and in part collected by myself. Of that which I obtained myself, some was gathered in the immediate vicinity of Cambridge, but much of it came either from Wood's Holl, Mass., or from Newport, R. I. The material which I obtained at Newport was collected at the Newport Marine Laboratory during the summer of 1890, and consisted of specimens of Idotea, Evadne, and Pontella; that which I got at Wood's Holl was collected at the United States Fish Commission Station during a brief period which I spent there in the summer of 1889, and included much of the material which I used in studying the eyes of Decapods. For the opportunities of collecting, both at Newport and Wood's Holl, I am indebted to Dr. Alexander Agassiz. I also desire to express my thanks to Prof. M. McDonald, the United States Commissioner of Fish and Fisheries, for many courtesies shown me while at the government station at Wood's Holl.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXV.

Essentially the same *methods* as those which I used in investigating the eyes in the lobster were employed in studying the eyes in other Crustaceans. As these methods have been described at some length in my paper on the lobster's eye (Parker, '90^a, pp. 3, 4), further mention of them in this connection is unnecessary.

Before proceeding to an account of the eyes in Crustaceans, a few statements should be made concerning the use of terms. In the following anatomical descriptions, I have very generally adhered to the older and more established terms. It must be admitted that some of these, on account of their derivation, are not entirely satisfactory, but because of their general acceptance I have chosen to retain them rather than to attempt to replace them by new ones.

The term *retinula*, the use of which varies with different writers, was introduced by Grenacher ('77, p. 17), who employed it to designate the rhabdome and the group of cells by which this structure is surrounded. Subsequently, Patten ('86, p. 544) used the same term as a name for a single cell of the group to which Grenacher gave the name retinula. In my paper on the eyes of the lobster I followed Patten's usage, but in the present paper I have decided to employ the term as originally defined by Grenacher, and to designate the individual cells in the retinula as *retinular cells*, — a translation of the term already used for this purpose in many German publications.

The greater part of the present paper is taken up with descriptions of the eyes in different Crustaceans. The amount of detail thus collected is considerable, and might appear at first sight to include many unimportant particulars; but the number of observations recorded is justifiable, I believe, on the ground that the majority of them bear more or less directly upon the solution of the principal question dealt with in the paper.

The following statements will make clear the character of this question. It is now well recognized that the retina in compound eyes is composed of a number of similar units or ommatidia, and that each ommatidium consists of a cluster of cells regularly arranged around a central axis. With very few exceptions, the different ommatidia in the retina of any given Crustacean agree with one another in the number and arrangement of their cells; in other words, in a given retina any ommatidium is the structural duplicate of any other. This uniformity suggests the idea of a structural type, and already a number of such types have been described. Some of these find representatives apparently only in the ommatidia of a single species, but more frequently the type characterizes a genus, family, or even a sub-order. Types differ from one another, either in the number of their cells or in the arrangement of these cells. Of these differences, the one which involves a variation in the number of cells is the more fundamental. This difference, however, has probably arisen by the gradual modification of an ancestral type, and, granting this, it follows that the ommatidia of one type are genetically connected with those of other types. This leads directly to the statement of the principal question, namely, *What are the means by which ommatidial types are modified, and what is the significance of the changes through which these types pass?*

This question, although easily stated, is not so easily answered; the facts presented in the following pages cannot be said to settle it, and yet they seem to me to increase materially the possibilities of its solution.

A partial answer to at least the first portion of the question has already been suggested (Parker, '90[a], pp. 56–58); it can be briefly stated as follows. There is reason for believing that those ommatidia which are composed of a small number of cells more closely resemble the ancestral type than those composed of many cells. Granting this statement, one would naturally expect that the more complex ommatidia had been derived from the simpler ones by an increase in the number of their elements. Perhaps the most natural method by which this increase could be accomplished would be by the further division of the cells already forming the ommatidium. Consequently, cell division in this sense seemed to me to afford a sufficient means for the modification of ommatidial types. In the present paper it is in part my purpose to show precisely to what extent cell division can be said to have modified ommatidia, and to determine whether any other factors have been involved in this process.

THE RETINA.

The retina in those Crustaceans in which its development has been studied originates as a thickening in the superficial ectoderm. At least three types of retinal structure can be distinguished, depending upon the ultimate form which this thickening assumes.

The FIRST TYPE which will be described is in several particulars the simplest, and probably represents a primitive form from which the other two are derived. This type is characteristic of the eyes in Decapods, Schizopods, Stomatopods, Isopods, the Nebaliæ, and the Branchiopodidæ, and is represented by a simple thickening in the superficial ectoderm.

Branchiopodidæ. — In the eye of adult specimens of Branchipus the retina is a lenticular thickening occupying the inner concavity of the distal end of the optic stalk. Near its edges the retina is directly continuous with the adjoining hypodermis. Its proximal face is bounded by a basement membrane which is also continuous with the corresponding membrane of the hypodermis, and its distal face is closely applied to the inner surface of the superficial cuticula. Thus the retina in the adult has in every respect the appearance of a simple thickening in the hypodermis.

The way in which the retina originates in Branchipus confirms the opinion that this organ has the simple structure suggested in the foregoing paragraph. The development of the retina in this genus has been studied by Claus ('86, p. 309), whose account can be summarized as follows. In that part of the head from which the optic stalks eventually arise, the ectoderm becomes considerably thickened; this thickening is subsequently divided into a superficial and a deep portion; the latter sinks into the head and becomes a part of the central nervous system; the former retains its external position and is converted into the retina. In Branchipus, therefore, the retina originates as a simple ectodermic thickening which retains its superficial position throughout the life of the individual. This method of origin, and the position permanently retained by the retina, are the two principal characteristics of the first retinal type.

Isopoda. — In adult specimens of Idotea irrorata, as sections perpendicular to the external surface of the eye show (Plate V. Fig. 49), the retina bears the same relation to the hypodermis as it does in Branchipus. Similar structural relations occur also in the eyes of Idotea robusta and of young specimens of Serolis Schythei.

The development of the retina in Isopods has been observed by Dohrn and Bullar. As early as 1867, Dohrn ('67, p. 256) described the eye in Asellus as originating in connection with a thickening in the lateral wall of the head, presumably in the ectoderm of that region. The details of the development of this organ were not followed on account of the continual increase of pigment. Bullar ('79, pp. 513, 514) in a paper on parasitic Isopods described the development of the retina in Cymothoa. His account is substantially as follows. In the course of the development of the cerebral ganglion, when this structure is separated from the superficial ectoderm, the latter remains on the exterior of the embryo as a layer of considerable thickness. From this superficial layer is developed the retina, i. e. all parts of the eye which in the adult lie between the basement membrane and the corneal cuticula.

I have studied a few stages in the development of the eyes in Idotea robusta. The retina in this species originates as a simple thickening in the superficial ectoderm, in essentially the same manner as Bullar has observed in Cymothoa.

The retina in Isopods, both in respect to its method of development and its general structure in the adult, is unquestionably a representative of what I have called the first type of retinal structure.

Nebaliæ. — In Nebalia, as the figures given by Claus ('88, Taf. X. Figs. 8 and 17) show, the retina and adjoining hypodermis are directly continuous, and the former presents all the characteristics of a simple thickening in the hypodermis.

Stomatopoda. — In an adult specimen of Gonodactylus which I examined, the relation between retina and hypodermis was the same as in Nebalia.

Nothing is known, I believe, of the development of the retina in either the Nebaliæ or the Stomatopods. The structure of the eyes in the adults of both groups, however, shows very conclusively that their retinas belong to the same structural type as those of Branchipus.

Schizopoda. — In describing the development of Mysis chamelio, Nusbaum ('87, pp. 171–185) states that the retina arises from a thickening in the superficial ectoderm, and adds that its formation, so far as his observations extended, was not complicated by an involution.

In Mysis stenolepis, a Schizopod whose eyes I have studied, the retina and hypodermis in the adult are directly continuous, as in Branchipus. This relation is what would be expected from the method of development described by Nusbaum.

Decapoda. — Carrière ('85, p. 169), in his account of the eyes in Astacus, showed very clearly that in the adult the retina and hypodermis formed a continuous layer. This relation was subsequently observed by me in Homarus (Parker, '90^a, p. 5), and I have since seen the same condition in Gelasimus, Cardisoma, Cancer, Hippa, Palinurus, Pagurus, Cambarus, Crangon, and Palæmonetes. There is, therefore, considerable ground for the support of Carrière's generalization, that the relation of the retina to the hypodermis as shown in Astacus is characteristic of all Decapods.

The development of the retina has been more fully studied in Decapods, perhaps, than in any other group of Crustaceans. Nevertheless, the accounts given by various writers are by no means in agreement, but differ in several important particulars. In a former paper (Parker, '90^a, pp. 31–43), I devoted considerable space to the discussion of these accounts, and I shall therefore not reopen the subject here. Suffice it to say, that since the publication of the paper referred to nothing has transpired to alter my belief that the retina in Decapods originates as a simple thickening in the superficial ectoderm.

In a recent preliminary communication by Lebedinski ('90) on the development of a marine crab, Eriphya, a brief description of the origin of the eye is given. This description, however, is so very much condensed that it is not easily understood, and since the author himself confesses that, on account of the complexity of the subject, a description without figures must be almost unintelligible, it would be unwise to hazard a presentation of his views. I shall therefore pass over this paper without further comment.

The evidence advanced in the course of the preceding paragraphs leaves no doubt in my mind that the retinas in the Branchipodidæ, the Nebaliæ, the Isopods, Stomatopods, Schizopods, and Decapods, belong to the same structural type, and that this type is represented by a thickening in the external ectoderm (hypodermis), which retains permanently its superficial position.

The SECOND RETINAL TYPE is more complicated than the first, and differs from it in that the retina does not retain its position at the surface of the body, but becomes buried beneath a fold of integument. Our knowledge of this type is largely due to the researches of Grobben ('79). The type is represented in the eyes of the Apusidæ, the Estheridæ, and the Cladocera.

Estheridæ. — In adult specimens of Limnadia Agassizii the two lateral eyes are rather closely approximated, and occupy a position in the ventral anterior portion of the animal's body (Plate IV. Fig. 33). The relation of the eye to the surface of the body can be seen most satisfactorily in sagittal sections. In such a section (Fig. 35) the eye has the appearance of a stalked structure which projects anteriorly into a cavity, the optic pocket (*brs. oc.*); this pocket communicates with the exterior by means of a small opening (*po. brs.*), the optic pore. The free surface of the stalked portion of the eye is covered with a delicate cuticula, which, after being reflected from the base of the stalk over the inner surface of the wall of the pocket, becomes continuous at the pore of the pocket with the superficial cuticula. The retina (Fig. 35, *r.*) occupies the greater portion of the optic stalk. Its distal face is bounded by the delicate cuticula already mentioned, and its proximal face is limited by a basement membrane (*mb. ba.*). This membrane becomes indistinct as the base of the stalk is approached, but the retina itself is apparently continuous in this region with the layer of cells which rests on the cuticular wall of the optic pocket, and which finally unites at the pore of the pocket with the superficial hypodermis. Thus the retina may be said to be continuous with the hypodermis.

The structure of the eyes in Limnadia Agassizii is such that they can be described as stalked eyes which have been surrounded by a fold of the integument, so as to become enclosed within a space, the optic pocket, which communicates with the exterior only by means of the optic pore.

An eye of essentially this structure has been described by Grobben ('79, p. 255) in Limnadia Hermanni, Limnetis brachyurus, and Estheria ticinensis, and in the last genus enough of the development of the eye was observed to indicate that the optic pocket was formed by the growth of a fold of integument over the optic stalk.

Apusidæ. — In Apus, according to Grobben ('79, p. 256), the plan of the eye is essentially similar to that in the Estheridæ. The eyes project into an open pocket, the cavity of which permanently communicates with the exterior. Judging from the figure given by Claus ('86, Taf. VII. Fig. 11, compare p. 366), the right and left retinas in Apus are not so close to one another as in the Estheridæ (compare Plate IV. Fig. 34).

Cladocera. — The structure and development of the retina in the Cladocera has been carefully studied by Grobben. My own observations on this group have been limited to a single genus, Evadne, and as this genus is not very favorable for the determination of the general relations of the retina I must rely almost entirely upon Grobben's descriptions.

In the development of Moina, according to Grobben ('79, p. 253), the retinal thickening is covered by a fold of the integument in such a manner that an open optic pocket is produced, as in Limnadia. By the closure of what corresponds to the optic pore, this pocket eventually loses its connection with the exterior, and becomes reduced to a closed sac on the distal face of the retina. With the closure of the sac, the continuity of the retina with the superficial hypodermis becomes interrupted.

In other Cladocera, especially the genera Sida and Daphnia, Grobben has found evidence to believe that the eyes are of essentially the same structure as in Moina. In a majority of the Cladocera the two compound eyes coalesce even more completely than in Limnadia.

In the development of Moina, as the preceding description indicates, the eye passes through a phase which closely resembles the permanent condition in Limnadia. The eye in the latter may therefore be interpreted as representing a stage in the phylogeny of the eye in Moina.

In accordance with the facts presented in the foregoing account, the second retinal type can be described as one in which the retina does not retain its primitive external position, but sinks below the surface of the animal and becomes covered by a fold of the integument. The optic pocket thus formed may remain permanently open, as in the Apusidæ and Estheridæ, or may become closed and partially obliterated, as in the Cladocera. The right and left retinas either remain separated, as in the Apusidæ, or become closely approximated, as in the Estheridæ, or fused, as in the Cladocera.

The minor modifications which this retinal type presents are not without importance. Bearing in mind the general statement that the compound eyes in Crustaceans are separate, paired, superficial structures, it is evident that the eyes in the Apusidæ, in which the retinas are separate and the optic pocket permanently open, depart only slightly from the primitive condition. In the Estheridæ, in which the two retinas are closely approximated, the eye is farther removed from the original type; but not so far as in the Cladocera, in which not only the two retinas are fused, but the optic pocket is closed and partially obliterated, thus entirely disconnecting the retina from the hypodermis. The three groups — the Apusidæ, the Estheridæ, and the Cladocera — may consequently be taken to represent a series in the differentiation of the second retinal type. That this series is a natural one, and that it culminates in the Cladocera, is shown from the fact that in the development of Moina, and perhaps many other Cladocera, the eyes pass through stages which reproduce the essential features of the permanent condition in the Apusidæ and Estheridæ.

In the THIRD RETINAL TYPE, as in the more differentiated form of the second, the retina is completely separated from the hypodermis.

The method by which the separation is here accomplished is not by the closure of an involution, as in the second type, but by a process the nature of which will be described in the following pages. The third type is represented by the eyes in Amphipods, and possibly in Copepods.

Amphipoda. — The peculiar relation which the retina bears to the hypodermis in Amphipods can be easily seen in Gammarus. In this genus, as Carrière ('85, pp. 156–160) has clearly demonstrated, the retina lies immediately below the hypodermis, and is separated from the latter by a well defined structure, the corneo-conal membrane (Fig. 1, *mb. crn'con.*). This membrane, although visible with perfect clearness, is nevertheless extremely delicate, and has the appearance of a single lamella. I believe, however, that its structure is more complex, and that it is composed of two very intimately united membranes, one of which is produced by the retina, the other by the corneal hypodermis. This belief is based upon the fact that at the edge of the retina the apparently single membrane separates into what may be considered its two constituents. One of these becomes the basement membrane of the general hypodermis, and the other, which I have called the capsular membrane, passes over the edge and proximal face of the retina, and is finally reflected over the optic nerve (Fig. 1, *mb. n. opt.*). In addition to the capsular membrane, the eye in Gammarus possesses still another membrane (Fig. 1, *mb. ba.*). This is a delicate lamella, which is approximately parallel to the deep face of the eye at a level between the rhabdomes and retinular nuclei (compare Fig. 2), and which consequently divides the space within the capsular membrane into two chambers, a larger distal and a smaller proximal one. At its periphery this intercepting membrane unites with the capsular membrane.

The corneo-conal and capsular membranes in Gammarus show no evidence of being perforated, but together constitute a closed capsule, which separates the retina from all adjoining tissues except the optic nerve. Both membranes are composed apparently of a homogeneous substance, in which I have never been able to distinguish any trace of cells. It is therefore probable that these membranes are cuticular.

The intercepting membrane, unlike either the capsular or the corneo-conal membrane, is pierced by a great number of holes, through which the proximal ends of the retinular cells project. This membrane, therefore, has the form of a meshwork. According to Carrière ('85, p. 158) it is composed of numerous connective-tissue cells, but this statement is not confirmed by my own observations. In depigmented sections of the retina the intercepting membrane had the appearance of a delicate lamella, in which I was unable to find any trace of cells. Not unfrequently the nuclei of certain accessory pigment cells (Fig. 2, *nl. k'drm.*) appear to touch the membrane, and even at times to lie with their long axes parallel to it, but in no case could these nuclei be said to be *in* the membrane. In sections of the retina from which the natural pigment had not been removed, it was often difficult to decide whether a given nucleus was *in* the membrane or only *next to* it. Possibly appearances such as these have led Carrière to believe that the membrane was cellular. My own opinion is, that the intercepting membrane, like the other two membranes, is a cuticula, and does not contain cells.

From the foregoing account, it will be seen that in an adult Gammarus the retina lies immediately under an undifferentiated corneal hypodermis, and is enclosed, excepting where the optic nerve emerges from it, by a non-perforated cuticular capsule. The space within this capsule is divided by a perforated cuticular membrane into a large distal and a small proximal chamber.

In Hyperia, judging from the figure given by Carrière ('85, p. 161, Fig. 123), the retina has essentially the same structure as in Gammarus. The intercepting membrane is in a position proximal to the rhabdomes and distal to the retinular nuclei. The layer of pigment cells, which Carrière ('85, p. 161, Fig. 124) apparently considers the intercellular membrane itself, in my opinion marks only approximately the position of that membrane. Probably in Hyperia, as in Gammarus, these cells rest on the distal face of the intercepting membrane.

In Phronima each side of the head is occupied by two eyes, instead of one, contrary to the condition in the more typical Amphipods. Of the two eyes, one is dorsal, the other lateral. This difference in position affords a convenient means of distinguishing them. The lateral eye presents all the essential structural features of the single eye in Gammarus (compare Carrière, '85, Figs. 125 and 121). The dorsal eye, although differing considerably in shape from the lateral one, is nevertheless constructed upon the same morphological plan. Its most important peculiarity is the shape of its intercepting membrane and the adjoining structures. In the dorsal eye the intercepting membrane, instead of lying in a plane nearly parallel with the external surface of the retina, as in the lateral eye, is cone-shaped. The axis of this cone corresponds to the axis of the eye; its apex is near the brain, and its base faces the external surface of the eye (compare Claus, '79, Taf. III. Fig. 20, and Taf. VII. Fig. 58). The ommatidia are arranged approximately parallel to its principal axis; distally, they terminate in the region of its base; proximally, they end either at its apex or on its lateral walls near the apex. The rhabdomes lie within the cavity of the cone, i. e. they are distal to the intercepting membrane, as in other Amphipods. The retinular nuclei cover the apical portion of the external surface of the cone, i. e. they are proximal to this membrane. These nuclei are covered externally by a second cone-shaped membrane, which separates them from the surrounding tissue. This membrane occupies the position of the capsular membrane of other Amphipods, and is unquestionably homologous with it.

The fact that both the lateral and dorsal eyes in Phronima are constructed upon the same plan as the single eye in Gammarus, supports the view that these two eyes have arisen by the division of a primitively single retina into two parts, and the subsequent independent differentiation of each part.

As the preceding account shows, in all Amphipods whose eyes have been studied carefully, the retinas conform to one structural type well exemplified by Gammarus. In this type the retina is characterized by two peculiarities: first, it is not continuous with the hypodermis, but lies immediately below that layer; and secondly, it possesses what appear to be two basement membranes, the capsular and the intercepting membranes. The significance of these peculiarities will be discussed in the following paragraphs.

The separation of the retina from the hypodermis is characteristic of only the more mature conditions of the eye in Amphipods; for as Pereyaslawzewa ('88, p. 202) has shown in Gammarus, and Rossiiskaya ('89, p. 577, and '90, p. 89) has demonstrated in Orchestia and Sunamphitoë, the retina originates as a thickening in the superficial ectoderm, in the same manner as in the majority of Crustaceans. So far as I am aware, however, no one has observed the detachment of the retina from the hypodermis, a process which must take place before the adult condition is reached. In the figure of the developing eye in Gammarus given by Pereyaslawzewa ('88, Plate VI. Fig. 120), the distal portion of the retinal thickening contains almost nothing but developing cones. In sections of my own from a corresponding region in a young specimen of Gammarus, the distal portion of the retina contains not only developing cones, but also isolated nuclei, which occasionally lie between the cones, but more frequently occur in positions distal to them. These nuclei are as numerous in the centre of the distal face of the retina as on its edges, and at this stage can always be easily distinguished from the nuclei of the cone cells. I believe they represent the nuclei of the corneal hypodermis. The retina proper is probably separated from this hypodermis by delamination; at least, the corneo-conal membrane is formed at a stage slightly older than that last mentioned, and, judging from the appearances at this stage, its formation is not accompanied by any folding of the hypodermis or retina, but is the result of a differentiation in place. Unfortunately, none of the specimens which I studied showed any steps in the formation of the corneo-conal membrane, and I am therefore uncertain as to the exact method of its growth.

Of the two membranes in the basal portion of the retina of Gammarus, presumably only one corresponds to the basement membrane of other Crustaceans. The position occupied by the two membranes, as well as their structure, serves to indicate which is the true basement membrane. At first sight one might suppose that the capsular membrane, at least in its proximal portion, corresponds to the basement membrane, but this interpretation is not probable, for the reason that the capsular membrane is not pierced by the fibres of the optic nerve, a characteristic of the true basement membrane of the eye. I therefore believe that the intercepting membrane, since it is perforated by these fibres, is the homologue of the basement membrane, and that that portion of the capsular membrane which might be regarded as a basement membrane is in reality merely the cuticular sheath of the optic nerve.

So far as I can foresee, the only objection to be urged against this interpretation of the intercepting membrane is found in its relation to the retinular nuclei. These nuclei in the eyes of almost all other Crustaceans lie on the *distal* side of the basement membrane. Granting that the intercepting membrane is the basement membrane, one must admit that in Amphipods they lie on the *proximal* side of this membrane. This admission might at first sight appear to offer an obstacle to the homology which I have suggested; but it can be made with consistency, I believe, provided one can show that the position of the retinular nuclei is not necessarily fixed. That such is the case is evident from the following facts. In Decapods the retinular nuclei usually occupy a position in their cells distal to the rhabdome. In Porcellio, as Grenacher ('79, Taf. IX. Fig. 96) has shown, they have a more proximal position, lying in the same transverse plane as the rhabdome itself. In Serolis they are midway between the rhabdome and the basement membrane. These conditions show, I believe, that the retinular nuclei may occupy very different positions in their cells, and that the step from the condition shown in Decapods to that shown in Serolis is not greater than that from Serolis to the Amphipods. It seems to me, therefore, that the objection suggested at the beginning of this paragraph is almost without weight. This conclusion, moreover, is supported by the fact that in Idotea (Plate V. Fig. 49) the retinular nuclei lie proximal to the basement membrane, whereas in the majority of other Isopods they are distal to that membrane.

From the preceding discussion, I conclude that the retina in Amphipods originates as a simple thickening in the superficial ectoderm, and that this thickening subsequently becomes separated, probably by a process of delamination, into a deeper portion, the retina proper, and a more superficial portion, the corneal hypodermis. The latter alone retains its original connection with the adjacent hypodermis. Of the two membranes present in the basal portion of the eye in Amphipods, that which I have called the intercepting membrane is homologous with the basement membrane of the retina in other Crustaceans, and that which has been designated as the capsular membrane is in large part the cuticular sheath of the optic nerve.

Copepoda. — The retinas in the Branchiura and Eucopepoda, the two divisions of the Copepods, present such different structural conditions that for purposes of description it is better to consider them separately.

Branchiura. — In adult specimens of Argulus, the retina is completely separated from all surrounding tissue, excepting the optic nerve, by an intervening blood space (Plate II. Fig. 11, *cœl.*). This peculiar condition was first clearly described by Leydig ('50, p. 331), although as early as 1806 Jurine ('06, p. 447) remarked that the eye in this genus was contained in a transparent membranous sac, which apparently contained a fluid, and Müller ('31, p. 97) some twenty-five years later described the retina as separated from the "cornea" by an intervening space filled with fluid. It remained, however, for Leydig to determine the extent of this space, and to demonstrate that the fluid which it contained was blood. The more essential features of Leydig's description have since been confirmed by Claus ('75, pp. 254–256).

The development of the eye in Argulus has not been studied with sufficient fulness to allow one to determine the relation of its retina to the hypodermis. But from the strong resemblance which the eye in the adult bears to that in Amphipods, it is probable that the course of development in the two cases is not unlike. Probably the retina in Argulus originates as a thickening in the superficial ectoderm, and subsequently not only suffers delamination, as in the Amphipods, but becomes actually withdrawn from the superficial layer (corneal hypodermis).

If this course of development really takes place, the various structures in the eye of an adult Argulus can be easily homologized with those in Amphipods. Thus the corneal hypodermis and corneal cuticula of Amphipods would probably be represented by the hypodermis and cuticula dorsal to the eye in Argulus (Fig. 11). The basement membrane of this hypodermis would correspond to the corneal component of the corneo-conal membrane of Amphipods, and the conal constituent would be represented by what is called the preconal membrane in Argulus (Fig. 11, *mb. pr'con.*). Proximally, the preconal membrane becomes continuous with the sheath of the optic nerve (Fig. 11, *mb. n. opt.*), the equivalent of the capsular membrane of Amphipods. The basement membrane of the retina in Argulus, as in Amphipods, is the membrane pierced by the fibres of the optic nerve (Fig. 11, *mb. ba.*).

Grobben ('79, p. 258) has suggested that possibly the eye in Argulus is of the same type of structure as in Phyllopods, but I do not share in this opinion for the following reasons. In Estheria, the delicate cuticula which covers the optic stalk is morphologically a portion of the outer surface of the body, and, as I hope to show subsequently, is subtended by a true corneal hypodermis. There is no corneal hypodermis beneath the preconal membrane of Argulus. Moreover, there is nothing in the eye of Argulus to correspond to the optic pocket of the Estheridæ, or to the optic sac of the Cladocera, except the circumretinal blood space, and it seems to me very improbable that this space was once a cavity in communication with the exterior, and afterwards became converted into a blood space. I therefore believe that the plan of the eye in Argulus is not similar to that in the Phyllopods, but rather that it represents a modification of the type presented by the Amphipods. The satisfactory determination of this question can be settled, however, only by embryological evidence.

Eucopepoda. — In adult specimens of those true Copepods which possess rudiments of the lateral eyes, — the Pontellidæ and Corycæidæ, — the retina is apparently separated from the hypodermis. In the Corycæidæ it usually lies at some considerable distance from the hypodermis, and in Pontella the two structures, although near one another, are nevertheless not continuous.

The development of the lateral eyes in the Corycæidæ and Pontellidæ has not been studied, and consequently it cannot be stated with certainty whether the retinas in these Crustaceans originate from the hypodermis or not. In the metanauplius larva of Cetochilus, a Copepod which as an adult has no lateral eyes, Grobben ('80, p. 262) has described a pair of thickenings, which extend from the superficial ectoderm of the antero-lateral part of the head to the brain. These thickenings are present only in the early stages of development, and represent the unsevered connection between the brain and the superficial ectoderm. They closely resemble the developing lateral eyes of Branchipus, and Grobben has therefore very justly considered them rudiments of the lateral eyes. If the rudiments of the lateral eyes in Cetochilus develop from the superficial ectoderm, it is probable that the lateral eyes in other Copepods have a similar origin.

To which of the three retinal types already described the eyes in Copepods belong is not easily decided. The absence of any indication of an optic pocket, either in the development of what Grobben considers the rudiments of the lateral eyes in Cetochilus, or in the fully formed eyes in other genera, seems to me to preclude the possibility of these eyes belonging to what I have described as the second type. The separation of the retina from the hypodermis prevents them from being classed with the first type, and, especially in the case of the Branchiura, brings them into close relation with the third type. It is my opinion, that, if the lateral eyes in Copepods are not representatives of a fourth type, essentially different from the three already described, they must be considered members of the third retinal type.

Certain species of Cumaceæ, Ostracods, and Cirripeds possess optic organs which probably represent the compound eyes of other Crustaceans; but so far as I am aware, the relation of these structures to the hypodermis is unknown. It is therefore impossible to state whether those eyes represent other retinal types, or belong to one of the three already described.

According to the preceding account, three retinal types can be distinguished in the compound eyes of Crustaceans. In the first of these the retina is a simple thickening in the superficial ectoderm (hypodermis). This type is characteristic of the eyes in Isopods, the Branchiopodidæ, the Nebaliæ, Stomatopods, Schizopods, and Decapods. In the Isopods, the eyes are sessile; in the other groups of the first type, they are borne on the distal ends of movable optic stalks.

In the second type, although the retina, as in the first type, originates as a thickening in the superficial ectoderm, it ultimately becomes enclosed within an optic pocket. This may remain permanently open, as in the Apusidæ and Estheridæ, or it may become closed, as in the Cladocera. In the Apusidæ, so far as I am aware, the eyes are not capable of motion, and in the Estheridæ they are, if at all, only slightly movable. In the Cladocera, where the second type probably reaches its greatest differentiation, the retina is remarkable for the freedom of its motion.

In the third type the retina originates from thickened hypodermis, which subsequently separates into two layers, the corneal hypodermis and the retina proper (a layer of cones and retinulæ). This separation is accomplished either by the formation of a corneo-conal membrane, as in Amphipods, or by what I believe to be an actual withdrawal of the retina proper from contact with the hypodermis, as in Copepods. Only in the representatives of the extreme modification of this type, the Copepods, are the eyes movable.

The course of development taken by each of the three types very clearly indicates their mutual relations. Evidently the first type is a primitive one, and since the first steps in the development of the second and third reproduce the permanent condition of the first, these two may therefore be considered derivatives from the first. It is interesting to observe that in the simpler condition of each type the retina is fixed, whereas in the more differentiated form it has become movable. The sinking of the retina into the deeper parts of the body, as represented in the second and third types, may have been induced by the protection thus obtained for the eye. After the three types were differentiated, each one seems to have been modified in a special way to give rise to a movable retina.

ARRANGEMENT OF THE OMMATIDIA.

The ommatidia in the retinas of some Crustaceans are so few in number that they can scarcely be said to be grouped according to any system. Where they are numerous, however, they are arranged upon one or the other of two plans. These may be designated the hexagonal and tetragonal plans of arrangement. In the hexagonal plan the imaginary outline of the transverse section of an ommatidium is a hexagon, and each ommatidium, excepting those on the edge of the retina, is surrounded by six others. In the tetragonal arrangement the ideal transverse section of an ommatidium is a square. Each of the four sides of this square is occupied by one of the four faces of an adjoining ommatidium.

The arrangement of the ommatidia can usually be determined by a careful inspection of the external surface of the eye; this determination is considerably facilitated by the presence of a facetted cuticula. Sometimes the form of a single facet is sufficient to indicate the plan of arrangement. Thus, hexagonal facets have never been observed except in connection with the hexagonal plan of arrangement. Circular facets are likewise known to occur only with this method of grouping. Square facets, on the other hand, may accompany either the hexagonal or tetragonal arrangement of deeper parts.

The hexagonal arrangement is apparently characteristic of the ommatidia in all Crustaceans,[1] except the Decapods. In the Decapods, as will be shown presently, the ommatidia are arranged either upon the hexagonal or the tetragonal plan. Before proceeding, however, to a description of the arrangement of the ommatidia in Decapods, it would be well perhaps to call attention to the rather peculiar grouping of these structures in Gonodactylus, a Stomatopod.

For a clear understanding of the arrangement of the ommatidia in this Crustacean, it is necessary to have some previous knowledge of the shape of its optic stalk. In Gonodactylus the stalks are elongated cylinders, the distal ends of which are rounded. In alcoholic specimens the stalks in an undisturbed position rest with their longitudinal axes approximately parallel with the chief axis of the animal, and with their distal ends directed forward. The retina occupies the free end of the stalk. Dorsally it extends over the distal half, ventrally over only the distal third of the stalk.

The ommatidia in Gonodactylus are of two kinds, large and small, which are always easily distinguishable from each other, although they differ in no essential respect except size. The large ommatidia are definitely arranged in six rows, which extend as well defined bands from the dorsal posterior edge of the retina anteriorly over its rounded distal end, and posteriorly over its ventral surface to its ventral posterior edge. This band thus occupies both dorsally and ventrally the median portion of the retina, and separates the remaining retinal surface into two parts, one on either side of the stalk. In alcoholic specimens this median band is readily visible with the aid of a hand lens, and a little closer scrutiny shows that it is composed of six lines. These lines, of course, correspond to the six rows of ommatidia previously mentioned. The smaller ommatidia, on either side of the median band, are also arranged in lines parallel to those in the band; but, on account of their smaller size, the lines formed by them are not visible with an ordinary lens.

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[1] Judging from the figures as well as the statements made by the authors quoted, the hexagonal arrangement is characteristic of the ommatidia in the following Crustaceans (exclusive of the Decapods): *Branchipus* (Burmeister, '35, p. 531, Spangenberg, '75, p. 30), *Nebalia* (Claus, '89, Taf. X. Fig. 10), *Gammarus* (Sars, '67, p. 62), *Orchestia* (Frey und Leuckart, '47, p. 204), *Phronima* (Claus, '79, Taf. VI. Fig. 48), *Cymothoa* (Müller, '29, Tab. III. Figs. 5, 6, Bullar, '79, p. 514), *Lygidium* (Lereboullet, '43, p. 107, Planche 4, Fig. 2^b), *Serolis* (Owen, '43, p. 174), *Arcturus* (Beddard, '90, Plate XXXI. Fig. 4), *Anceus* (Hesse, '58, pp. 100 and 103, Dohrn, '70, Taf. VIII. Figs. 33, 34), *Squilla* (Milne-Edwards, '34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Leydig, '55, p. 411), and *Mysis* (Sars, '67, Planche III. Fig. 7, Grenacher, '79, Taf. X. Fig. 112). I have observed the hexagonal arrangement in the following genera: *Apus*. *Branchipus*, *Estheria*, *Evadne*, *Argulus*, *Gammarus*, *Caprella*, *Talorchestia*, *Idotea*, *Serolis*, *Porcellio*, *Sphæroma*, *Mysis*, and *Gonodactylus*.

The smaller ommatidia in Goniodactylus are arranged upon the typical hexagonal plan (see the left half of Fig. 93, Plate VIII.). The larger ones have a somewhat similar grouping, although the fact that they are in six longitudinal rows rather obscures their hexagonal arrangement. (See the right half of Figure 93, in which three rows, and a part of a fourth, of large ommatidia are shown.) The hexagonal arrangement is not disturbed, as might be expected, on the line which separates the larger from the smaller ommatidia, but both kinds form parts in a common system. That this is true can be seen from Figure 93, where it will be observed that the *centres* of any two small ommatidia lying in the same vertical line are as far apart as the *centres* of the corresponding larger ommatidia. Moreover, as I have demonstrated by actually counting the ommatidia of long parallel series, a vertical band which contains twenty-five large ommatidia has the same length as one composed of a corresponding number of small ones. The apparent difference in numbers at first sight presented by lines of the two kinds of ommatidia is principally due to the fact that the larger ommatidia are arranged in distinct rows, whereas the smaller ommatidia are so grouped that the individuals in one row are slightly interpolated between those of the two adjoining rows (compare Fig. 93).

In Decapods the ommatidia are arranged either upon the hexagonal or tetragonal plan. In the Brachyura,[1] as well as in three families of the Macrura, the Hippidæ, Paguridæ, and Thalassinidæ,[2] the arrangement of the ommatidia is invariably hexagonal. In the remaining macrurous Decapods[1] the ommatidia are grouped on the tetragonal plan. This last statement, however, is not without exceptions, for in Typton, and at times also in Galathea,[2] the hexagonal arrangement appears to prevail. An explanation of these exceptions will be offered in a subsequent paragraph.

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[1] The presence of hexagonal facets has been recorded in the following genera of Brachyura: *Portunus* (Will, '40, p. 7); *Ilia* (Will, '40, p. 7, Leydig, '55, p. 411); *Cancer; Maja; Carpilius* (Frey und Leuckart, '47, p. 204); *Herbstia, Dorippe,* and *Lambrus* (Leydig, '55, pp. 407, 410, and 411, respectively). This form of facet is present only when the ommatidia are hexagonally arranged. Leydig ('55, p. 411) states that the outline of each facet in *Dromia Rumphii* is square, but, as his description clearly indicates, the facets are arranged upon the hexagonal plan. As my own observations show, the ommatidia in *Cardisoma Guanhumi,* Latr., *Cancer irroratus,* Say, and *Gelasimus pugilator,* Latr., are hexagonally grouped.

[2] The outline of the corneal facets is stated to be hexagonal in the following genera: *Pagurus* (Swammerdam, '52, p. 88, Cavolini, '92, p. 130, Milne-Edwards,

Before attempting this explanation, however, it will be well to gain a precise idea of the relation of the hexagonal and tetragonal methods of arrangement. At first sight, it might appear that these two methods had no definite relations, and were simply characteristic of different Decapods. Such, however, is not the case; for, as the development of the lobster shows, the ommatidia in a *single* animal can be arranged at first according to one plan, and afterward according to the other. In the lobster the hexagonal arrangement characterizes the earlier stages of development, and is replaced only subsequently by the tetragonal grouping. A similar change also occurs in the spiny lobster. Thus, in Phyllosoma, the larva of either Palinurus or Scyllarus, the hexagonal facets observed by Milne-Edwards ('34, p. 115) afford unquestionable evidence of the hexagonal arrangement at this stage. In the adult condition, however, both of Palinurus and of Scyllarus, according to my own observations, the ommatidia are tetragonally grouped. In the common lobster and the spiny lobster, then, the hexagonal arrangement of the early stages is replaced by the tetragonal one in the adult. These ob-

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'34, p. 117, Will, '40, p. 7, Frey und Leuckart, '47, p. 204, Chatin, '78, p. 8); *Callianassa;* and *Gebbia* (Milne-Edwards, '34, p. 117). In *Pagurus longicarpus*, Say, and *Hippa talpoida*, Say, I have observed a hexagonal arrangement of the ommatidia.

[1] Judging from the figures given by various authors, the ommatidia of the following genera are characterized by the tetragonal arrangement: *Galathea* (Will, '40, Fig. III. c.); *Astacus* (Müller, '26, Tab. VII. Fig. 13, Leydig, '57, p. 252, Fig. 134, Reichenbach, '86, Taf. XIV. Fig. 226, Huxley, '57, p. 353); *Homarus* (Newton, '73, Plate XVI. Fig. 3, Parker, '90^a, p. 8); *Palæmon* (Grenacher, '79, Taf. XI. Fig. 118 A, Patten, '86, Plate 31, Fig. 115); *Penæus* (Patten, '86, Plate 31, Fig. 75). As my present observations have shown, the tetragonal arrangement is characteristic of the ommatidia in *Palinurus Argus*, Gray, *Cambarus Bartonii*, and *Palæmonetes vulgaris*, Say.

[2] According to Chatin ('78, p. 13) the outline of the facet in *Typton* is hexagonal. Presumably the arrangement of the ommatidia in this genus is upon the hexagonal plan. In *Galathea*, according to the figures given by Patten ('86, Plate 31, Fig. 116), the ommatidia are hexagonally arranged, although it must be borne in mind that Will's ('40, Fig. III. c.) figure of the facets in *Galathea strigosa* affords unmistakable evidence of a tetragonal arrangement.

servations appear to me to afford considerable evidence in favor of the view that the hexagonal arrangement is phylogenetically more primitive than the tetragonal.

Granting this conclusion, a number of otherwise exceptional observations can be explained. Thus, as long ago as 1840, Will ('40, p. 7) called attention to the fact that in Astacus, where the ommatidia are normally arranged upon the tetragonal plan, facets near the edge of the retina are often irregularly hexagonal. The edge of the retina is well known to be the last part produced, and therefore it is probably the part least differentiated. Admitting the hexagonal arrangement to be a primitive one, it is only natural to expect that, if it persists at all, it will persist in the less modified portion of the retina. Hexagonal facets also occur on the periphery of the retina in Homarus, and are to be explained, I believe, in the same way.

On the assumption that the hexagonal plan is primitive, the occurrence of a few genera with ommatidia hexagonally arranged, in a group in which the tetragonal arrangement is the rule, can also be explained. In Typton, for instance, the hexagonal plan obtains, although in almost all Crustaceans closely related to it the tetragonal system prevails. This condition may be explained, however, by the fact that the eyes in Typton show evident signs of degeneracy, due in all probability to the parasitic habits of the Crustacean. If the hexagonal arrangement represents an early ontogenetic phase in the development of Decapods related to Typton, it would be natural to expect that in Typton itself, where the normal development of the eyes is interrupted by parasitism, this arrangement would persist permanently.

In Galathea, as I have already mentioned in a note on page 63, the ommatidia according to Will are arranged tetragonally; according to Patten, hexagonally. At first sight these observations might appear to be irreconcilable, but such is not necessarily the case. So far as I have been able to ascertain, Patten does not mention the name of the species which he studied. Possibly he may have examined some other than G. strigosa, the one from which Will's figures were drawn. In such an event, a difference in the arrangement of the ommatidia may have been characteristic of the two species, although, if both possessed well developed eyes, this difference would be somewhat anomalous. If this is not the true explanation, it is still possible that the specimens studied by Patten were somewhat immature, in which case the hexagonal arrangement might very naturally be present. From what has been said, I think it must be evident that the apparent contradiction in Will's and

Patten's statements is not so serious as might at first be supposed, and that, admitting the relations already mentioned between the two plans of arrangement, the observations of these two writers can be explained without supposing either of them to be wrong.

The probable method of rearrangement by which the hexagonal plan is converted into the tetragonal has been suggested in a previous paper (Parker, '90^a, p. 50). It involves two changes: the conversion of the hexagonal outline of the ommatidium, as seen in the corneal facet, into a square one, and the slipping of the rows of ommatidia one on the other, so that the lines which bound the four sides of each facet finally form parts of two series of lines which cross each other at right angles.

A condition somewhat intermediate between the hexagonal and tetragonal arrangement is shown in the retina of Crangon (Plate X. Fig. 123). In this genus the outlines of the ommatidia as seen in the facets are square, although their arrangement suggests the hexagonal type. The permanent grouping of the ommatidia in Crangon represents a stage slightly in advance of the condition seen in some young lobsters (compare Parker, '90^a, Plate IV. Fig. 55), and the particular features in which this advance is shown are two. First, the distal retinular nuclei in Crangon (Fig. 123) are grouped in pairs, more as they are in adult lobsters, and not in circles of six, as in young ones (compare Parker, '90^a, Figs. 5 and 55). Secondly, the arrangement of the ommatidial centres in reference to the hexagonal plan is more symmetrical in the young lobster than in Crangon, where the rows of ommatidia have apparently slipped somewhat upon one another so as to resemble more nearly the condition in the adult lobster.

I have been unable to determine with certainty what occasions the change from the hexagonal to the tetragonal arrangement. Apparently it accompanies an excessive growth on the part of the individual ommatidia. In the lobster, for instance, the ommatidia rearrange themselves between the times when the young animal is one inch and eight inches long. During this period the ommatidia increase about ten times in length and about five times in breadth. The increase is especially noticeable at their distal ends, and particularly in the cone cells. In young lobsters of one inch in length (Parker, '90^a, Plate IV. Fig. 55), the space between the cones of adjoining ommatidia is considerable; in adults, it is proportionally very much less (compare Parker, '90^a, Plate I. Fig. 5), and the cones are crowded against one another. Under these conditions, the hexagonal arrangement apparently gives way to the tetragonal. So far as I am aware, the tetragonal arrangement occurs only in connection with this crowding of the cones, a condition found for the most part only in macrurous Decapods.

In accounting for the rearrangement of the ommatidia, the eyes in the Stomatopod Gonodactylus afford some important evidence. As I have previously mentioned, the ommatidia in this genus are of two sizes. The larger ones have several of the peculiarities characterizing the tetragonal arrangement: their facets are generally square; they are arranged in single lines, and these lines, so far as the relations of the individual ommatidia are concerned, show evidences of having slipped upon one another. The smaller ommatidia have hexagonal facets, and are clearly arranged according to the hexagonal plan. The larger ommatidia are rather closely packed; the smaller ones are arranged with more open space between them (compare Plate VIII. Fig. 93). In this genus, then, as in the lobster, the tetragonal arrangement occurs in connection with the crowding of the ommatidia.

How an increase in size, accompanied by a crowding of the retinal elements, can induce the change in arrangement which seems to follow it, I am at a loss to explain. Nevertheless, the two phenomena appear to be in some way connected.

From the preceding discussion concerning the arrangement of the ommatidia, the following conclusions can be drawn. The ommatidia, when numerous enough, present one of two plans of arrangement, the hexagonal or the tetragonal. The hexagonal plan is phylogenetically the older, and is characteristic of the eyes of all Crustaceans except some families of the macrurous Decapods, especially the Galatheidæ, Palinuridæ, Astacidæ, and Carididæ. In these the hexagonal arrangement is usually replaced by the tetragonal; but in the adults of some species, especially those in which the eyes are partially rudimentary, the hexagonal arrangement persists. The change from the hexagonal to the tetragonal arrangement is connected apparently with an increase in size, and consequent crowding, of the ommatidia.

The Structure of the Ommatidia.

Each ommatidium, as I have previously mentioned, consists of a cluster of cells more or less regularly arranged about a central axis. The greatest number of kinds of cells which an ommatidium is known to contain is five. These are the cells of the corneal hypodermis, the cone cells, the proximal and distal retinular cells, and the accessory cells.

The cells of the corneal hypodermis are usually arranged in a very thin layer, and constitute the most superficial tissue in the retina. They either present no definite arrangement, as in Amphipods, or they are regularly grouped in pairs, one pair for each ommatidium, as in the majority of Crustaceans. On their external faces they produce the corneal cuticula. This is unfacetted in those Crustaceans in which the corneal cells are not regularly arranged and facetted when they are grouped in pairs.

The cone cells in each ommatidium are united to form the cone, a transparent body which extends from the corneal hypodermis proximally through the ommatidium at least as far as the rhabdome. The cone occupies the axis of the distal portion of the ommatidium.

The proximal retinular cells are usually limited to the proximal portion of the ommatidium. They are definitely arranged around the axial structure of that region, the rhabdome, and together with it form a single body, the retinula. The optic nerve fibres terminate in the proximal retinular cells.

The distal retinular cells are present in only the more differentiated ommatidia. They are two in number, and invest the sides of the cone distal to the plane at which this structure emerges from the retinula. When distal cells are present, the remaining cells of the retinula will be distinguished as proximal cells; when the distal cells are wanting, the other cells will be called simply retinular cells.

The accessory cells fill the space between the elements of an ommatidium, or between separate ommatidia. Their number is apparently inconstant, and they present a variety of forms. They may or may not contain pigment. Depending upon their source, two kinds can be distinguished, ectodermic and mesodermic.

In describing the ommatidia, I shall consider them according to the groups of Crustaceans in which they occur. Under each group the elements comprising the ommatidium will be described in the order in which they have just been mentioned.

My object in the following account is to determine, as far as possible, what the different kinds of ommatidial types are, and to define these types by a brief statement of the number and kinds of cells which characterize them.

Compound eyes are known to occur in some Ostracods, and in the larvæ of some Cirripeds, but their histological structure, I believe, has never been studied. I am therefore compelled to dismiss these two groups without further comment, and proceed with the description of the ommatidia in other Crustaceans. The order in which the groups will be considered is one which is intended to emphasize their relations only in so far as the structure of their ommatidia is concerned. Naturally, this order will vary somewhat from the one usually given in systematic treatises. I shall begin with the Amphipods.

Amphipoda.

Within recent years the more important types of eyes in the Amphipods have been studied with such care that the structure of their ommatidia is perhaps better known than that of any other large group of Crustaceans. My own observations do little more than confirm the accounts already published.

The species of Amphipods whose eyes I have examined are Gammarus ornatus, M. Edw., Talorchestia longicornis, Say, and an undetermined species of Caprella. Of these the specimens of Gammarus and Caprella were collected at Nahant, Mass., where I also obtained several sets of eggs representing stages in the development of the former. Examples of Talorchestia were kindly supplied me from the collections in the Museum.

The *corneal hypodermis* in Amphipods was first satisfactorily described by Claus ('79, p. 131) in his account of the eyes in Phronima. It is represented in this genus by a layer of undifferentiated cells lying between the corneal cuticula and the membrane which limits the distal ends of the cone cells. A corneal hypodermis similar to that in Phronima has likewise been described by Mayer ('82, p. 122) in Caprella and Protella, by Carrière ('85, p. 156) in Gammarus, by Claus ('87, p. 15) in the Platyscelidæ, by Della Valle ('88, p. 94) in the Ampeliscidæ, and by Watase ('90, p. 295) in Talorchestia. I have also identified this structure in Gammarus, Caprella, and Talorchestia.

In Gammarus, as Carrière ('85, p. 156, Fig. 121) has clearly shown, the corneal hypodermis at the edges of the retina is directly continuous with the general hypodermis. According to my own observations this condition is not only met with in Gammarus, but also in Caprella and Talorchestia.

In Phronima, according to Claus's figures ('79, Taf. VI. Figs. 48 and 49, *Ma Z.*), the arrangement of the cells in the corneal hypodermis bears no definite relation to the subjacent cones; the distal end of each cone presents an area which is covered by about a dozen hypodermal cells. In Gammarus I have observed (Plate I. Figs. 2 and 3) an essentially similar distribution of the hypodermal cells; as in Phronima, the number of cells which cover the area of each cone is about twelve. A corneal hypodermis of this same character also occurs in Talorchestia, although in this instance the number of cells over a cone is only about nine.

According to Watase ('90, p. 295), in the species of Talorchestia which he studied there were only two cells in the corneal hypodermis opposite each cone, or, as he expresses it, under each facet. When compared with the results recorded in the preceding paragraph, this observation appears somewhat striking, and the more so since two, the number of cells recorded, is the usual number found under each facet in other Crustaceans. If Watase's observation be correct, the relation which would thus be established between this Amphipod and other Crustaceans would be an interesting one. The desirability of confirming Watase's observation must, therefore, be evident; but unfortunately he has not given the name of the species of Talorchestia which he studied, and I have therefore not been able to verify his statement. In the only species of this genus which I have examined, viz. T. longicornis, the arrangement of the cells in the corneal hypodermis is very different from that described by Watase.

The conclusions which I draw from the preceding account are, that in the eyes of Amphipods a corneal hypodermis is present, and the cells composing it are usually not arranged with regularity.

The peculiar bodies observed by Schmidt ('78, p. 5) in the membrane between the corneal hypodermis and the retina proper in Phronima, and considered by Claus ('79, Taf. VI. Figs. 48, 49, *B. nu.*) as nuclei, are apparently not represented in other Amphipods. Their significance is still a matter of doubt.

The *corneal cuticula* in Amphipods has been described by almost all observers as unfacetted.[1] According to Della Valle ('88, p. 94), however, in some of the Ampeliscidæ this cuticula is facetted, and Watase ('90, p. 295) has also observed facets in Talorchestia. But with these two exceptions the corneal cuticula of Amphipods has been described as smooth. The absence of facets from Amphipods is naturally accounted for by the absence of a definite arrangement among the cells of the corneal hypodermis.

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[1] An unfacetted corneal cuticula has been recorded in the following genera of Amphipods: *Amphithoe* (Milne-Edwards, '34, p. 116); *Caprella* (Frey und Leuckart, '47^a, p. 103); *Cyamus* (Müller, '29, p. 58, Frey und Leuckart, '47, p. 205); *Gammarus* (Müller, '29, p. 57, Frey und Leuckart, '47, p. 205, Pagenstecher, '61, p. 31, Sars, '67, p. 61, Leydig, '78, p. 235, Grenacher, '79, p. 109); *Hyperia* (Gegenbaur, '58, p. 82, Grenacher, '79, p. 111, Carrière, '85, p. 160); *Phronima* (Pagenstecher, '61, p. 31, Schmidt, '78, p. 5, Claus, '79, p. 131); *Talitrus* (Grenacher, '79, p. 109); and the *Platyscelidæ* (Claus, '87, p. 15). I have observed an unfacetted corneal cuticula in *Gammarus*, *Caprella*, and *Talorchestia longicornis*.

In the genus Tenais, the systematic position of which is probably somewhere between the Amphipods and Isopods, the corneal cuticula is stated by Müller ('64, p. 2) to be facetted, at least in the males. According to Blanc's ('83, p. 635) more recent observations, however, it is claimed to be unfacetted.

The *cones* in Amphipods have long been known to be segmented. The number of segments of which each cone is composed has been differently stated, however, by different observers. According to Claparède ('60, p. 211), the cones in Hyperia are each composed of four segments. This also is the number given by Sars ('67, p. 61) and by Leydig ('79, p. 235) for Gammarus. Both Hyperia and Gammarus have since been carefully studied, and these observations are now known to be inaccurate. Claparède was perhaps influenced in his statement by his belief that all cones were composed of four cells. Sars was probably misled by the supposed fact that in Gammarus the cone is surrounded by four bands of pigment, which sometimes give it the appearance of being divided into four segments.

The actual number of segments in the cone of Amphipods is two. This number was first recorded by Pagenstecher ('61, p. 31) for the cones of Phronima. Pagenstecher believed, however, that the cones in this Crustacean increased in numbers by division, and that they showed no indication of being composed of two segments except when they were undergoing this process. I need scarcely add that subsequent investigations have not confirmed Pagenstecher's belief. Cones composed of two segments have been observed in some six or seven genera of Amphipods.[1]

The *retinula* in Amphipods is stated by different observers to consist of either four or five cells. Five have been seen by Grenacher ('74, p. 653) and Carrière (85, p. 160) in Hyperia; by Grenacher ('79, p. 112), Claus ('79, Taf. VIII. Fig. 65), and Carrière ('85, p. 164) in Phronima; and by Mayer ('82, p. 122) in Caprella.

In Gammarus, Sars ('67, p. 61) observed that the cone had four longitudinal bands of pigment on it. Grenacher ('79, p. 110) took this as an indication that there were at least four retinular cells in the ommatidium of this genus, but he was unable to satisfy himself as to whether there were a greater number or not. Carrière ('85, pp. 156, 157) easily identified the four cells first seen by Sars, and in favorable cases observed what he thought might be indications of a fifth cell. In Gammarus ornatus, as the present observations show, the retinula is certainly always composed of five cells, one of which, as Carrière observed, is usually much smaller than the other four (compare *cl. rtn.'*, Figs. 4–7).

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[1] In *Caprella* (Mayer, '82, p. 122), in *Gammarus* (Grenacher, '79, p. 110, Carrière, '85, p. 156), in *Hyperia* (Grenacher, 74, p. 652), in *Oxycephalus* (Claus, '71, p. 151), in *Phronima* (Schmidt, '78, p. 5, Grenacher, '79, p. 112, Claus, '79, p. 130), in *Talorchestia* (Watase, '90, p. 296), and in the *Platyscelidæ* (Claus, '87, p. 15). In *Gammarus ornatus, Talorchestia longicornis,* and *Caprella,* each cone is composed of two cells.

In Talorchestia, according to Watase ('90, p. 296), the retinula is composed of only four cells. I have studied T. longicornis with the purpose of determining the number of retinular cells, and I find that, although there are four large retinular cells, there is also one small one, which is even more reduced than in Gammarus. Hence I conclude that the total number of retinular cells in an ommatidium of Talorchestia is five, not four.

Claus's statement ('71, p. 151), that in Oxycephalus the retinula is usually composed of four cells, is probably inaccurate, as Grenacher ('79, p. 114) suggests; and the same is perhaps true of Della Valle's ('88, p. 94) observation, that in the Ampeliscidæ the retinulæ contain only four cells each. It is therefore probable that the retinula in all Amphipods is composed of five cells, although possibly in some exceptional cases the number may be four.

The retinular cells in Gammarus envelop the sides of the cone, as Carrière suspected, and extend distally as far as the corneal hypodermis (Plate I. Fig. 2). In Hyperia and Phronima, according to the description and figures given by Carrière ('85, p. 161, and Fig. 128, p. 165), these cells appear to be limited to the proximal part of the retina.

The *rhabdome* in Amphipods, first described by Pagenstecher ('61, p. 30) as the cylindrical element in the eye of Phronima, presents a very simple structure. In Hyperia, according to Grenacher ('77, p. 31), it is a simple rod-like body, composed of five rhabdomeres, one for each retinular cell. In Phronima, as Claus ('79, p. 128) has shown, the rhabdome is a tubular structure with five sides. Each side of the tube, as can be seen in the figure given by Carrière ('85, p. 165, Fig. 128), corresponds to a rhabdomere. In Gammarus locusta, Grenacher ('77, p. 111) has shown that, in transverse section, the distal end of the rhabdome is cross-shaped. In G. pulex, according to Carrière ('85, p. 157), the distal end of the rhabdome in section shows four rays, the proximal five. In Carrière's opinion, these rays indicate the five rhabdomeres. In Gammarus ornatus, the species which I have studied, the rhabdome (Plate I. Fig. 6, *rhb.*) is cross-shaped in transverse section throughout its length. Each rhabdomere has the form of an elongated plate, which is folded on its longest axis, so that its halves are at right angles to each other. In the rhabdome, the four rhabdomeres lie so that their folded edges occupy the axis of the ommatidium. Each of the four large retinular cells rests in the furrow produced by the folding of a rhabdomere (compare Fig. 6). The fifth retinular cell always lies at the end of one arm of the cross-shaped rhabdome. The two rhabdomeric constituents of that arm usually separate slightly, so as to allow the small retinular cell to slip in between them. Possibly this cell produces a small rhabdomere, as the corresponding cell in G. pulex does; but if such is the case, the rhabdomere must be a very small one, for I have not been able to discover it. A rhabdome of essentially this structure occurs in Talorchestia.

As the preceding account shows, the rhabdome in Amphipods always presents some indication of the number of rhabdomeres of which it is composed. This number is usually five, although it is possible that in Gammarus it may be only four.

In addition to the cells which have thus far been described as entering into the composition of the retina in Amphipods, certain other cells may be present. These may be embraced under the one head of *accessory pigment cells.*

In Gammarus, as Carrière ('85, p. 159) has shown, the space between the ommatidia is filled with rather large cells, the nuclei of which are usually visible with ease (Fig. 2, *nl. h'drm.*). These cells extend from the basement membrane very nearly, if not quite, to the corneal hypodermis. In the fresh condition they contain a whitish opaque pigment. On account of their having no definite arrangement, it is difficult to estimate their number, but there are probably two or three for each ommatidium. Cells similar in position to these have been described by Watase ('90, p. 296) in Talorchestia.

In Hyperia there are apparently three kinds of accessory pigment cells. One kind occurs in the region of the basement membrane (Carrière, '85, p. 161, Fig. 124, *m.*); another kind surrounds the proximal portion of the cones (Carrière, '85, p. 161); a third kind is applied to the retinulæ, and, according to Carrière, exactly equals in number the cells of the retinula itself. Possibly the cells which Grenacher ('79, p. 112) described as lying at the distal end of the retinula in Hyperia belong to this third kind, although, as must be remembered, Grenacher states that there are only two such cells for each ommatidium.

These three kinds of accessory pigment cells, with the possible exception of those which surround the retinula, occur in the lateral eyes of Phronima (Carrière, '85, p. 164).

Almost nothing is known about the source of the accessory pigment cells in Amphipods. Those in Gammarus have no resemblance to the loose mesodermic tissue which lies in the neighborhood of the eye, and they are probably derived from the original ectodermic thickening which gave rise to the retina. Although some of the accessory pigment cells in Hyperia and Phronima have been called connective-tissue cells (Claus, '79, p. 125, Carrière, '85, p. 160), a name which might be taken to imply that they have come from a mesodermic source, nothing is really known about them which would be inconsistent with an ectodermic origin.

From the foregoing account of the ommatidia in Amphipods the following summary can be made: cells of the corneal hypodermis not definitely arranged, from about nine to twelve, — possibly two to each ommatidium; cone cells, two; retinular cells, five, — possibly in some cases four; accessory pigment cells (ectodermic?) present. Of these last there may be only one kind, as in Gammarus and Talorchestia, or there may be three kinds, as in Hyperia.

Phyllopoda.

The ommatidia in the eyes of Phyllopods present at least two structural types, one of which obtains in the Branchiopodidæ and Apusidæ, the other in the Estheridæ and Cladocera. On account of the greater convenience, the eyes in the Apusidæ and Branchiopodidæ will be considered first, then the eyes in the Estheridæ, and finally those in the Cladocera.

Branchiopodidæ and Apusidæ. — The ommatidia in these two families, and especially in the Branchiopodidæ, have been carefully studied by a number of competent investigators; their structure is consequently well known.

The material which I used in studying these eyes consisted of specimens of Branchipus, probably B. vernalis, Verrill, which I had collected in the neighborhood of Philadelphia, and which had been preserved for some time in strong alcohol. Through the kindness of Dr. W. A. Setchell, I was also able to examine a specimen of Apus lucasanus, Packard.

A *corneal hypodermis* has been described by Claus ('86, pp. 321, 322) in Branchipus and Apus. In Branchipus torticornis, according to Claus, the nuclei of the hypodermal cells are arranged around the distal end of each cone in circles of six; each nucleus participates in three circles, so that there are in reality only twice as many hypodermal cells as there are ommatidia. The corneal hypodermis in the eye of Branchipus vernalis (Plate IV. Fig. 30, *nl. h'drm.*) is similar to that described by Claus in B. torticornis. According to Patten ('86, p. 645), a corneal hypodermis is present in Branchipus Grubii, but the cells, instead of being regularly placed, as in either Branchipus torticornis or B. vernalis, are stated to be indefinitely arranged.

The *corneal cuticula* in Apus is described as unfacetted by Müller ('29, p. 56), Burmeister ('35, p. 533), Zaddach ('41, p. 46), and Frey und Leuckart ('47, p. 205). In Branchipus stagnalis the cuticula is smooth according to Spangenberg ('75, p. 30), marked by concavo-convex facets according to Grenacher ('79, p. 114), and smooth externally but facetted internally according to Leydig ('51, p. 295). This difference of opinion is probably due to the fact that in this species the facets are so poorly developed that their form can be determined only with difficulty. In Branchipus vernalis, although the corneal cuticula is facetted, the facet is not thickened in its centre, but has the form of a simple concavo-convex elevation, as described by Grenacher in B. stagnalis. In Branchipus paludosus according to Burmeister ('35, p. 531), in B. torticornis according to Claus ('86, p. 320), and in B. Grubii according to Patten ('86, p. 645), the corneal cuticula is unfacetted.

The *cone* in Branchipus, as Spangenberg ('75, p. 30) first demonstrated, is composed of four segments. This observation has since been confirmed by Grenacher ('79, p. 115), Claus ('86, p. 320), and Patten ('86, p. 645). In Branchipus vernalis (Fig. 31, *con.*) the cone, according to my observation, consists of four segments. The cellular nature of each segment was first clearly stated by Grenacher. Each cone in Apus, according to both Grenacher ('79, p. 115) and Claus ('86, p. 321), is composed of four cells.

The *retinula* in both Apus and Branchipus consists of five cells. This number has been seen in both genera by Grenacher ('74, p. 653) and by Claus ('86, p. 319). Spangenberg, however, ('75, p. 31) counted *four* nuclei in the retinula of Branchipus. Since these unquestionably represent the nuclei of the retinular cells, and since these cells are usually five in number, Spangenberg's enumeration is probably inaccurate. Possibly he was influenced when counting the nuclei by his belief that the number four was characteristic of many structures in the ommatidium. In Branchipus vernalis (Plate IV. Fig. 32, *cl. rtn.'*) the retinula contains five cells.

The *rhabdome* in Apus is short; in Branchipus (Fig. 30, *rhb.*) it is relatively long. In transverse section (Fig. 32, *rhb.*) it is circular, or at times squarish, but never pentagonal, as might be expected from the fact that it is surrounded by *five* retinular cells.

The retina in B. vernalis contains no other cells than the three kinds already described. According to Claus ('86, p. 319), blood corpuscles may make their way into the base of the retina of B. torticornis.

From the preceding account, the number of cells in the ommatidia of the Branchiopodidæ and Apusidæ can be stated as follows: cells of the corneal hypodermis, usually two, possibly variable in number in some species; cone cells, four; retinular cells, five. In Branchipus torticornis the interommatidial space may contain blood corpuscles.

Estheridæ. — The species which I studied as a representative of this family was Limnadia Agassizii, Packard. This species can usually be obtained in great abundance during summer in small fresh-water pools in the neighborhood of Wood's Holl, Mass., where my material was kindly collected for me by Mr. W. M. Woodworth.

The external surface of the retina in Limnadia, as I have mentioned in my account of the general structure of the eye in this genus, is covered with an extremely delicate corneal cuticula. This cuticula does not show the least trace of facets.

Immediately below the corneal cuticula are numbers of small nuclei (Plate IV. Fig. 37, *nl. crn.*). These, from their position, are probably to be regarded as the nuclei of the corneal hypodermis. They are not regularly arranged, and, although they sometimes lie between the cuticula and the distal end of a cone, they more frequently occur next to the cuticula in the spaces between the cones.

As a rule, each *cone* in Limnadia is composed of *five* cells (Plate IV. Figs. 37 and 38). In this respect it resembles the cones in Estheria californica and E. tetracera described by Lenz ('77, p. 30). In Limnadia Agassizii, however, cones composed of *four* cells are not infrequently met with (compare Figs. 37 and 38). Grube's ('65, p. 208) observation that the cone in Estheria is composed of two segments is probably erroneous, but Claus's ('72, p. 360) statement that in Limnadia the cone consists of four segments may be accurate, contrary to the opinion of Lenz.

The *retinular cells* in Limnadia cover the greater part of the sides of the cones, and completely hide the rhabdome (Plate IV. Fig. 36). Their number can be determined in transverse sections in the region of the rhabdome. In such sections each rhabdome is surrounded by five retinular cells (Fig. 39, *cl. rtn.'*). Occasionally nuclei can be distinguished in the pigment about the base of the cone. These are probably the nuclei of the retinular cells.

Besides the elements thus far enumerated, the retina in the Estheridæ is not known to contain other kinds of cells. The cells in the ommatidia of this family are, therefore, as follows: cells of the corneal hypodermis, not regularly arranged; cone cells, usually five, sometimes four; retinular cells, five.

Cladocera.—The extreme minuteness of the ommatidia in the eyes of the Cladocera renders their study especially difficult. In an undetermined species of Evadne which I have studied, the ommatidia are comparatively large, and in this respect are especially favorable for investigation. In the particular specimens which I used, however, I was entirely unsuccessful in all attempts to differentiate the nuclei. Although I tried a number of dyes and reagents, I was never able to make these structures visible. In consequence of this, there are several important questions concerning the eyes in the Cladocera which I have not been able to answer.

It is reasonable to believe that a corneal hypodermis much like that in Limnadia is present in Evadne, but, probably on account of my inability to stain the nuclei, I have seen no traces of it.

The *cones* in Evadne are very clearly composed of five segments (Plate IV. Figs. 41, 42). At their distal ends the cone cells are expanded so that their peripheral membranes (Fig. 41, *mb. pi'ph.*) are in contact with one another. At this level, however, the substance of the cone proper is collected about the axis of the ommatidium. Proximally the peripheral membranes of each cone contract, and under these circumstances the cavity of each cone cell is apparently filled completely with the differentiated material of the cone itself (Fig. 42).

A cone composed of five segments has been observed in a considerable number of Cladocera. Thus it is known to occur in Bythotrephys (Leydig, '60, p. 245, Claus, '77, p. 144), Daphnia (Spangenberg, '76, p. 522, Grenacher, '79, p. 117), Polyphemus, Evadne (Claus, '77, p. 144), Podon (Grenacher, '79, p. 117), and Leptodora (Carrière, '84, p. 678). Weismann's assertion ('74, p. 364) that the cone in Leptodora is composed of four segments is disproved by Carrière's later observations, and

Claus's statement ('76, p. 372) that the same number of segments occurs in the cone of Sida is probably erroneous. There is, therefore, reason to believe that the cones in the Cladocera are always composed of five segments.

The composition of the *retinula* in Cladocera, so far as I am aware, has never been fully worked out. In Evadne, on account of the relatively large size of the ommatidia, the number of cells in the retinula can be determined. At the proximal end of the cone, this structure is surrounded by *four* distinct masses (Fig. 43). The regularity with which these masses occur leaves no doubt as to their number. Each one probably represents a retinular cell. In transverse sections made through the rhabdome (Plate IV. Fig. 45), this structure is surrounded by *five* bodies, each one of which I take to be a retinular cell. It is therefore probable that the retinula of Evadne is composed of five cells, four of which approach nearer the surface of the eye than the fifth.

In Evadne I have seen no evidence of the existence of other cells than those belonging to the cone and retinula. According to Carrière ('84, p. 678), the interommatidial space in Leptodora contains a number of cells which envelop the cones more or less completely. These are probably to be regarded as accessory pigment cells.

From the foregoing account the following general statement can be made for the ommatidia in the Cladocera: corneal hypodermis, not observed; cone cells, five; retinular cells, five (in Evadne); accessory pigment cells present (in Leptodora).

Copepoda.

I have studied the lateral eyes in Pontella and Argulus, as representatives of the Copepods. As is well known, the eyes in these two genera differ greatly in structure, and I shall therefore describe them separately, beginning with the eyes in Pontella.

Eucopepoda. — The species of Pontella which I studied was extremely abundant at Newport in August, 1890. This animal was so transparent when living, that the general structure of its eyes could be ascertained by a simple microscopic inspection of it. In addition to its median eye, which occupies a ventral position, it possesses a pair of lateral eyes (compare Claus, '63, Taf. III. Fig. 5) situated one on either side of the sagittal plane at the antero-dorsal angle of the head.

Each lateral eye in Pontella, as Claus ('63, p. 47) has already stated, is provided with a spherical lens (Plate II. Fig. 18, *lns.*), which is usually firmly attached to the superficial cuticula. Immediately behind this lens, and in fact covering much of its proximal face, is a rather irregular mass of cells, the retina. In the living animal the cells of the retina contain a great quantity of black or reddish black pigment. This coloring matter, however, is so readily soluble in alcohol, that in specimens preserved in that fluid all traces of it disappear. The optic nerve (*n. opt.*, Fig. 18), an imperfectly defined bundle of fibres, emerges from the retina near its posterior dorsal edge, and passes directly backward to the brain.

The lenses of the two lateral eyes in Pontella are so near each other that their median faces are almost in contact (compare Plate III. Fig. 29). The retinas of the two eyes, as Claus ('63, p. 47) has observed, are united with one another on their median faces, and so intimately that they are apparently incapable of independent motion.

The two retinas together may be rotated on their lenses through an angle of about forty-five degrees. The plane of this rotation corresponds to the sagittal plane of the body, and the rotation is accomplished by two pairs of muscles, one for each retina (compare Claus, '63, Taf. III. Fig. 6). One pair of these muscles is shown in Figure 18. They occupy a plane approximately parallel to the sagittal plane of the body, and the effects of their contractions must be apparent from their positions. When both muscles are relaxed, the retina occupies a position substantially as shown in Figure 18. By the contraction of the posterior muscle, the retina may be drawn upward and backward over the surface of the lens, till its axis, instead of pointing dorsally, is directed forward and upward at an angle of about forty-five degrees with its original position. The retina is not usually held for any great length of time in this position, but is soon returned by the contraction of the anterior muscle to its normal place. The backward motion of the retina is accomplished with such rapidity that the animal has the appearance of winking. The forward motion is rather slower.

Each lens in Pontella is composed of concentric laminæ (Plate III. Fig. 29, *lns.*). A considerable portion of its distal surface is intimately connected with the superficial cuticula (Plate II. Fig. 18), although a line of demarcation between lens and cuticula can always be distinguished.

When the anterior half of the body of Pontella is boiled in a strong aqueous solution of potassic hydrate, and afterwards subjected to the action of concentrated nitric acid, all the soft parts are dissolved, and only the very resistant chitinous structures remain. In specimens treated in this way, the lenses retain their firm connection with the superficial cuticula, and differ in appearance from those in the living animals only in that their concentric lamellæ are somewhat more distinct. The fact that the lens is composed of concentric layers indicates that it is secreted, and the resistance which it offers to reagents is weighty evidence in favor of its chitinous nature. In my opinion, therefore, the lens in Pontella is a chitinous secretion.

The development of the lens in Pontella is rather peculiar. Apparently a new lens is formed with each moulting of the general cuticula; at least, in a rather large proportion of the number of individuals examined, the lenses were abnormally small, having a diameter of one third or even one fourth of that shown in Figure 18. Moreover, in all such individuals the superficial cuticula was correspondingly thin and delicate, and when the animal was subjected to boiling potash, the segments of its body and appendages separated with a readiness never observed in specimens with large lenses. There can be no doubt, I believe, that the small lenses are always accompanied by thin cuticula, a relation which is to be explained by the immature condition of both structures.

The smaller lenses differ from the larger ones in only one important particular besides that of size. They are not in contact with the superficial cuticula. This relation can be determined better in optical sections than in actual ones, for in the latter the position of the lens is usually somewhat changed by the resistance which it offers to the knife. The centre of the small lens occupies a position relatively the same as that of the large lens, the space between the surface of the small lens and the external cuticula being filled with a cellular mass. This mass, as seen in optical sections, apparently envelops the lens on all sides, and is undoubtedly composed of the cells which secrete that structure. As the lens increases in size, the cells are probably excluded from the region between it and the cuticula, and as they retreat cement the lens to the cuticula. Upon the completion of the lens, the cells which have shared in producing it probably withdraw slightly from it to form the hypodermal thickenings which occur beneath the adjoining cuticula (Plate II. Fig. 18, and Plate III. Fig. 29, *h'drm.*). These thickenings are rich in nuclei, and often have delicate strands of protoplasm stretching to the surface of the lens (Fig. 18).

I believe that these facts justify the opinion that the lenses in the lateral eyes of Pontella are composed of chitin, that they are produced unconnected with the superficial cuticula, and that they are secondarily cemented to it. Like the cuticula itself, they are products of the hypodermis, a new lens being generated in all probability with each new formation of cuticula.

Lenses similar in position to those in Pontella have been identified in the lateral eyes of several other genera of Copepods. Gegenbaur ('58, p. 71) described such lenses in Sapphirina, and Leuckart ('59, p. 250) observed similar ones in the lateral eyes of Corycæus and Copilia. In all these genera the lenses, although biconvex, are not spherical, as in Pontella. Gegenbaur ('58, p. 71), following Leydig's generalization, believed that in Sapphirina the lenses were thickenings in the cuticular covering of the body, and Claus ('59, p. 271) considered them morphologically equivalent to a single corneal facet. Leuckart ('59, p. 250), without definitely committing himself as to the nature of the lens, states that in Copilia and Corycæus the lens is implanted in the superficial cuticula, and further describes it in Corycæus as composed of two parts, an outer and an inner. According to Grenacher ('79, p. 67), both parts can be identified in the lens of Copilia; the outer part is a portion of the superficial cuticula; the inner part, both in its optical properties and its behavior toward reagents, is unlike the cuticula. The inner part, however, contains no traces of cells, but is composed of a homogeneous substance, probably secreted. This view of the duplicity of the lens contrasts with the older idea of its origin as a thickening in the superficial cuticula.

It is possible that the lenses in the Pontellidæ and Corycæidæ are not homologous structures, but on account of their similarity I am inclined to consider them as such. Since in Pontella both parts are derived from the cuticula, I believe that a similar origin will be demonstrated for these parts in the Corycæidæ. The differences which Grenacher has pointed out between the two parts of the lens in Copilia do not necessarily oppose this view. It is possible that the cuticular secretion which forms the proximal part of the lens may originate separately from the other cuticula, as in fact it does in Pontella; and it may also be true, although this is not supported by the condition in Pontella, that the two parts, although both secretions of the hypodermis, may differ enough in their substance to account for all the peculiarities observed by Grenacher.

The *retina* and lens in Pontella are not separated by an intervening space as in the Corycæidæ, but are in immediate contact. The retina is composed of a mass of cells, the number and arrangement of which can be seen in the figures on Plate III. These figures represent a series of consecutive sections cut in planes transverse to the axis of the eye, i. e. parallel to the horizontal plane of the animal (compare Fig. 18, Plate II.). The series is complete in that it represents all the sections which pass through the retina. The most ventral section is shown in Figure 20, the most dorsal in Figure 29.

Immediately below the lens the central part of the retina is occupied by a roundish granular mass (Fig. 18, *con.*), which in the living animal is the only part without pigment. In transverse sections this mass is seen to consist of two bodies (*cl. con. 1*, and *cl. con. 2*, Fig. 25), which extend as far as to the lens (compare Figs. 25–27). Each body contains a nucleus (*nl. con.*, Figs. 25 and 27) and consequently represents a cell. From the position which the mass occupies, and from the fact that it contains no pigment, it represents, I believe, a cone, and the two cells of which it is composed are its two segments.

Claus ('63, p. 47) states that in Pontella each retina is provided with six or more small crystalline cones, but my own observations do not confirm this statement. The body which, on account of its position, I have described as the cone in Pontella, is probably homologous with what Dana ('50, p. 133) first described as the inner lens in Corycæus, and with what subsequent investigators have called the crystalline cones in Sapphirina (Gegenbaur, '58, p. 71) and Copilia (Leuckart, '59, p. 252). Nothing, I believe, is known of the cellular composition of the cone in these genera.

The arrangement of the elements in that portion of the retina which surrounds the cone in Pontella is not easily made out. The most conspicuous structures in this region are rod-like bodies, which probably represent rhabdomeres. Eight of these, arranged in three groups, are present in each retina. The largest group, composed of five rods, lies directly beneath the cone. The rods of this group have been numbered from one to five in the retina to the left in Figures 21, 22, and 23. Posterior to this group, in the same retina, is the sixth rod, seen in Figures 24, 25, and 26. Anterior to it are the seventh and eighth rods, seen in Figures 26, 27, 28, and 29.

The outlines of the cells to which these rods belong cannot always be distinguished; that there is a cell for each rod is evident from the fact that near each rod there is a large nucleus. The nucleus belonging to the cell from which the eighth rod was produced is shown in Figure 28 (*nl. rtn.'*); those belonging to the cells from which the sixth and seventh rods arose are indicated in Figure 26 (*nl. rtn'.*), and those belonging to the cells from which the central group of five rods came are seen, four in Figure 24 and one in Figure 25 (*nl. rtn.'*).

In addition to these nuclei, which judging from their positions and number are unquestionably the nuclei of the cells to which the rhabdomeres belong, the retina contains a number of smaller nuclei (Fig. 21, *nl. h'drm.*). These nuclei have been drawn in the figures of the various sections in which they occur, and probably represent undifferentiated cells.

To what extent the retina of Pontella can be resolved into ommatidia may be seen from the foregoing account. Evidently the two cone cells, the subjacent groups of five retinular cells, and probably some of the undifferentiated cells, are the equivalent of one ommatidium. The sixth cell, with its rod, is probably the representative of a second ommatidium, and the seventh and eighth cells are probably representatives of one, or perhaps two, more.

If this interpretation be correct, the cells in the one complete ommatidium in Pontella would be as follows: corneal hypodermis, undifferentiated; cone cells, two; retinular cells, five; undifferentiated pigment cells (ectodermic?) present.

Each retina in Sapphirina, according to Grenacher ('79, pp. 69, 70), contains one group of three rhabdomeres. These are accompanied, as in Pontella, by an equal number of large nuclei. The body designated at *y*, and perhaps some of those marked *x*, in Grenacher's figure of Sapphirina (Fig. 43), may also represent isolated rhabdomeres. In Copilia, Grenacher believes that the number of rhabdomeres in each retina is three. Possibly in this genus, as in Sapphirina, the body marked *x* by Grenacher (Taf. VI. Fig. 40) may represent an isolated rhabdomere. Grenacher's observations, when coupled with what I have seen in Pontella, show that in Copepods the number of retinal elements is open to considerable variation, and that what would correspond to the retinula in Sapphirina, and perhaps in Copilia, consists of a cluster of only three cells, instead of five, as in Pontella.

Branchiura. — The ommatidia in Argulus are rather small, and their structure is consequently imperfectly known. The specimens of this Crustacean which I studied were obtained from an aquarium in which the common Killifish, Fundulus heteroclitus, had been kept. I have not been able to determine the species to which these specimens belong.

The *corneal hypodermis* in Argulus is separated from the retina proper by a space filled with blood (Plate II. Figs. 11, 12, *cœl.*). The cells in this layer (Fig. 12, *h'drm.*), as in the corneal hypodermis of Amphipods, are not arranged in groups, but are irregularly scattered. On their distal faces they produce the corneal cuticula (Fig. 12, *cta.*), which, as Müller ('31, p. 97) observed, is without facets. Proximally they are separated from the blood space by the delicate corneal membrane (Fig. 12, *mb. crn.*).

The distal face of the retina proper in Argulus is bounded by a delicate preconal membrane (Figs. 11–13, *mb. pr'con.*) and its proximal face is limited by the basement membrane (Figs. 11–13, *mb. ba.*).

The most conspicuous objects in the retina are the *cones* (Fig. 11, *con.*), which lie with their distal ends usually somewhat below the preconal membrane (Fig. 13). Each cone, as Claus ('75, p. 256) has observed, is composed of four segments (Fig. 14). The segments correspond to cells, and although the cone itself terminates proximally before reaching the rhabdome, the cone cells form an axis free from pigment and extending from the cone to the rhabdome (compare Fig. 12). In depigmented sections the peripheral membranes of the cone cells (Fig. 13, *mb. pi'ph.*) can be distinguished as sharply marked lines which extend from the sides of the cone to the sides of the rhabdome. The intercellular membranes of the cone cells in the region between the cone and rhabdome are apparently marked by thickenings which appear in both longitudinal and transverse sections (compare Figs. 13 and 15). At the distal end of the rhabdome the four cone cells separate, and, after passing partly around the rhabdome, become lost in the adjoining tissue (Fig. 16, *cl. con.*). I have not been able to discover the nuclei of the cone cells.

It is difficult to determine the number of cells in the *retinula* of Argulus. Slightly below the proximal end of the rhabdome, the retinula is divided into five distinct pigmented masses (Fig. 17, *cl. rtn.'*). Since the rhabdome (Fig. 16, *rhb.*) is composed of five rhabdomeres, it is highly probable that the retinula consists of five cells; but I have not been able to determine with precision the outline and extent of these cells.

The nuclei which are visible in the retina of Argulus closely resemble one another. They are limited for the most part to two regions (Fig. 13), one near the level of the cones, the other near the basement membrane. Apparently there are no nuclei immediately below the preconal membrane. Those which are near the cones (Figs. 13, 14, *nl. h'drm.*), judging from their arrangement and position, probably represent interommatidial pigment cells. Those near the basement membrane (Fig. 13, *nl. rtn.'*) may be the retinular nuclei, as their position seems to indicate. For some distance proximal to the basement membrane, nuclei (Fig. 13, *nl. h'drm.'*) occur among the nerve fibres. Possibly they represent scattered cells in this region, but the strong resemblance which they have to the nuclei on the distal side of the membrane induces me to believe that they too are retinular nuclei, which, as in the Amphipods, have migrated to a position below the basement membrane.

The cells in the ommatidium of Argulus are as follows: cells of the corneal hypodermis, not arranged in definite groups; cone cells, four; retinular cells, probably five; accessory pigment cells probably present.

Isopoda.

The material which I used in studying the eyes in Isopods came from several sources. I collected specimens of Asellus and Porcellio in the neighborhood of Cambridge, and the two species of Idotea which I studied were obtained at Newport. Specimens of Serolis Schythei, Lütken, and of an undetermined species of Sphæroma, were kindly furnished me from the collections in the Museum.

The ommatidia in Isopods present two types of structure: one of these is characteristic of the eyes in a majority of the members of this group; the other, so far as is known, is represented only in the genus Serolis. These two types will be considered separately, and the one which is common to the greater number of Isopods will be described first.

The *corneal hypodermis* in the more common of these two ommatidial types was first identified by Grenacher. In Porcellio, according to this author ('79, p. 107), the proximal surface of each facet is covered with two comparatively thin cells. These are the cells of the corneal hypodermis. Bellonci ('81^a, p. 98, Tav. II. Fig. 11 n.) figures similar cells in the ommatidium of Sphæroma, and Beddard ('90, p. 368) concludes justly, I believe, that, of the four nuclei found near the distal end of the cone in Arcturus, two represent cone cells and two cells in the corneal hypodermis. In Idotea irrorata I have identified two cells in the corneal hypodermis for each ommatidium. The nuclei of these cells lie very near the nuclei of the cone cells (compare *nl. con.* and *nl. crn.* in Figs. 50 and 51, Plate V.). In an ommatidium of Porcellio, Grenacher ('79, pp. 107, 108) observed that the plane which separates the two cone cells also separates the two cells in the corneal hpyodermis. In Idotea, also, both kinds of cells are separated by a single plane.

The facetted condition of the *corneal cuticula* of Isopods was observed as early as 1816 by G. R. Treviranus ('16, p. 64), in wood-lice, and subsequently in the same animals by Lereboullet ('43, p. 107, '53, p. 119). The shape of the facets in different Isopods has given rise to some difference of opinion. According to Müller ('29, p. 42), in Cymothoa each has the form of a biconvex lens. Leydig ('64^a, p. 40) states, however, that in Oniscus the facets are concavo-convex with their hollow faces innermost. In Asellus, according to the figure given by Sars ('67, Planche VIII. Fig. 14), they are plano-convex with their flat faces innermost. These differences, although at first sight somewhat contradictory, are not matters of great importance, for it is probable that each time an Isopod sheds its cuticula and a new one is formed, the lens assumes, at successive stages of its growth, outlines which coincide very closely with those recorded by the different observers. Thus, an early stage would be represented by the concavo-convex lens described by Leydig, an intermediate stage by the plano-convex lens figured by Sars, and the final condition by the biconvex lens mentioned by Müller. Either this is the explanation of the differences, or the observations of Leydig and Sars are probably erroneous, for the results of the more recent investigations point to the conclusion that the facets in Isopods have the form of a biconvex lens. Facets of this shape have been seen by Grenacher ('77, p. 29) in Porcellio, and by Bellonci ('81^a, p. 98) in Sphæroma. According to my own observations, they also occur in Idotea, Asellus, Porcellio, and, as I shall show subsequently, in Serolis. In the four genera mentioned the inner face of each facet is distinctly convex; this is also true of the outer face in Asellus and Porcellio. In Serolis and Idotea (Plate V. Fig. 50), however, the outer face is so slightly curved that it is difficult to decide whether its curvature is that of the general corneal cuticula or one peculiar to the facet itself.

That the *cone* in Isopods is composed of two segments was first observed by Leydig ('64^a, p. 41, and '64, Taf. VI. Fig. 8) in Oniscus. According to this author, each segment is spherical. Each ommatidium, therefore, contains two spheres, and these, as Leydig's figure shows, are placed side by side immediately below the corneal facet.

It is now well known that in many Isopods, especially in the woodlice, the cone itself is nearly spherical, and its two segments would consequently be hemispheres, not spheres as figured by Leydig. How Leydig's statement of the spherical shape of the segments can be accounted for, is not apparent. Since the two spheres described by him occupy the same relative positions as the hemispherical segments of a normal cone, there is not much question in my mind that they represent these segments. Possibly their separation and spherical form may have been due to the swelling action of some reagent which Leydig may have used to make the tissue transparent. A cone composed of two segments has been observed by Sars ('67, p. 110) in Asellus, by Leydig ('78, p. 256) in Ligidium, by Grenacher ('77, p. 29) in Porcellio, by Bellonci ('81^a, p. 98) in Sphæroma, by Sye ('87, p. 23) in Jæra, and by Beddard ('90, p. 368) in Arcturus. In the three genera which I have examined, Idotea, Asellus, and Sphæroma, each cone consists of two segments.

These observations naturally lead to the conclusion that in all Isopods each cone is composed of two segments. To this general statement, however, there are two noteworthy exceptions, one recorded by Sars, the other by Beddard. Sars ('67, p. 110) has shown that, of the four ommatidia in each eye of Asellus aquaticus, three have cones composed each of two segments; in the fourth, however, the cone is divided into three parts. This observation has been confirmed by Carrière ('85, p. 155). It is important to observe that in the figure given by Sars ('67, Planche VIII. Fig. 12) the three parts of the cone are not of equal size; one is about as large as a single segment in the cones of the other three ommatidia, whereas the remaining two are each about half as large. In the eyes of the species of Asellus found about Cambridge, the ommatidia are usually twice as numerous as in the European species, A. aquaticus, and, so far as I could observe, the cones in the American species were always composed of only two segments. In Arcturus, according to the figures given by Beddard ('90, Plate XXXI. Figs. 1 and 4), cones of three segments are occasionally met with.

The cellular composition of the *retinula* in Isopods was first made out by Grenacher ('74, p. 653), who found that in Porcellio this structure consisted of seven cells. Distally these cells surround the cone; proximally they are continuous with the optic-nerve fibres. A retinula consisting of seven cells has also been demonstrated by Buller ('79, p. 513) in Cymothoa, and by Beddard ('88, p. 443) in Æga and Ligia. As Beddard ('88, Plate XXX. Fig. 13) has shown, the seven cells in the retinula of Æga pass through the basement membrane and become continuous with the nerve fibres. In Porcellio, as I have observed, the fibrous ends of the seven retinular cells not only can be identified as nerve fibres below the basement membrane, but each cell contains a well developed fibrillar axis (Plate V. Fig. 46, *ax. n.*), and I therefore conclude that in Porcellio all seven cells are functional as nervous elements.

In Idotea robusta, transverse sections of the retinula in the region where the rhabdome is thickest present the outlines of what seem to be *seven* retinular cells (Plate V. Fig. 48). In positions either distal or proximal to this, however, only *six* cells appear. These six cells pass through the basement membrane and taper into nerve fibres, and their nuclei, unlike the corresponding nuclei in other Isopods, occur in that part of the cell which is proximal to the basement membrane (Figs. 49 and 50, *nl. rtn'.*). The seventh body (Fig. 48, *cl. rud.*), in those sections in which it occurs, has in all essential respects the same appearance as any one of the adjoining six cells. It differs from these, however, in that it is usually somewhat smaller, and I therefore conclude that it is a rudimentary cell. It does not appear to contain a nucleus; granting, however, that it is a rudimentary retinular cell, one would look for its nucleus, not in the region about the rhabdome, but in the region of the nuclei of the other retinular cells, i. e. proximal to the basement membrane. Owing to the irregularity with which the fibrous ends of the retinular cells are arranged in this region, I have not been able to identify any nucleus with this rudimentary cell. Neither have I found any fibrous projections reaching from the rudiment of the cell toward the basement membrane such as might be expected provided the nucleus and a part of the rudimentary cell persisted below the membrane. Nevertheless, I believe, for the reasons already stated, that the retinula in Idotea robusta is composed of seven cells, one of which is extremely rudimentary.

In Idotea irrorata (Plate V. Figs. 53, 55) the retinula consists of only six cells, all of which possess fibrillar axes, and are therefore probably functional as nervous structures. In one retina of the several pairs of eyes which I examined, there was a single ommatidium with *seven* functional cells (Fig. 54). With this one exception, however, I have not been able to find any trace of the seventh cell in Idotea irrorata. In Arcturus, according to Beddard ('90, p. 368), the retinula is also composed of six cells.

In Sphæroma, Bellonci ('81, p. 98, Tav. II. Fig. 12) has figured and described a retinula consisting of *five* cells. These cells alternate with five other cells, which probably represent accessory pigment cells. If Bellonci's statement is correct, it must be admitted that the number of cells in the retinulæ of Isopods may be as few as five. My own observations, however, do not confirm Bellonci's account. In the species of Sphæroma which I have studied, there are *seven* cells in the retinula, four of which are large and three small (Plate V. Fig. 58). All these cells pass through the basement membrane; all the large ones, and certainly some of the small ones, are also connected with nerve fibres.

These observations indicate that in the Isopods the retinula is composed of either six or seven cells. If Bellonci's statements prove to be correct, this structure may be composed in some cases of only five cells, but my own observations are opposed to this view.

The *rhabdome* in Isopods presents two types of structure, one of which has been well described by Grenacher ('77, p. 30) for Porcellio scaber. In this species the rhabdome is composed of seven rhabdomeres, each of which remains in connection with the retinular cell which produced it. In transverse section the rhabdome has the form of a seven-pointed star, a ray corresponding to a rhabdomere. Each ray projects into its retinular cell, not between two cells. My own observations on Porcellio confirm Grenacher's statements. A second representative of this type of rhabdome has been described by Bellonci ('81, p. 98) for Sphæroma. Here, however, the rays, although they agree in number with the retinular cells, project *between* the cells, not into them.

The second type of rhabdome is well represented in the eye of Arcturus furcatus. In this species, according to Beddard ('90, pp. 368, 369), the distal portion of the rhabdome, although surrounded by *six* retinular cells, is bounded by *four* perpendicular sides. Each of the six cells appears from its position to contribute to the formation of the rhabdome, and yet in the greater part of this structure segments corresponding to rhabdomeres are not visible. In its proximal portion, however, the rhabdome, according to Beddard, is divided into six rhabdomeres, each of which is applied to its proper retinular cell. In Idotea robusta the rhabdome (Plate V. Fig. 48, *rhb.*) is nearly square in transverse section. So far as I have been able to discover, it does not show at its proximal end any indication of rhabdomeres.

Of these two types of rhabdome, the one in which the rhabdomeres are evident is probably more primitive than the one in which their individuality is almost, if not completely lost.

The retinas of Isopods may contain, in addition to those already mentioned, two other kinds of cells. Of these the one most frequently met with fills the space between ommatidia. Cells of this kind have been identified in Porcellio by Grenacher ('79, p. 107), and it is probable that the pigment cells described by Bellonci ('81, p. 99) as intervening between the retinular cells in Sphæroma belong to this class. I have observed interommatidial cells in Idotea; here they contain few or no pigment granules, but are easily recognized by means of their nuclei (Plate V. Fig. 54, *nl. h'drm.*).

The source of these cells is not definitely known, but there appears to be no evidence in favor of their having been derived from outside the retina. Grenacher believed that those in Porcellio are undifferentiated hypodermal cells; this interpretation probably holds good for those in Sphæroma and Idotea.

The hyaline cells, the second kind of accessory cells, have been identified by Beddard ('87, p. 235, '88, Pl. XXX. Fig. 9, *h.*) in Æga and Cirolana. Since these cells are best developed in the eyes of Serolis, a full description of their structure will be deferred until the account of the eyes in that genus is given.

The cells which characterize the ommatidia in Isopods (except Serolis) are as follows: cells of the corneal hypodermis, two; cone cells, two; retinular cells, seven, six, or possibly five. Undifferentiated hypodermal cells are sometimes present, and hyaline cells occur in a few genera.

The structural peculiarities of the *ommatidia in Serolis* were first described by Beddard ('84, pp. 339–341) about seven years ago. Recently Beddard's observations have for the most part been confirmed by Watase ('90), and it must now be admitted without question that the ommatidia in Serolis differ in several important respects from those of many other Isopods.

The material which I used in studying the eyes in this Crustacean consisted of advanced embryos and matured individuals of Serolis Schythei, Lütken. This material was collected in Patagonia by the Hassler Expedition, and was preserved in strong alcohol. Fortunately, it was in good histological condition, and sections prepared from it showed very clearly the finer structure of the eyes. My observations, as the following account will show, differ in no very important respects from those of Beddard and Watase.

Although Patten's generalization, that a *corneal hypodermis* was to be found in the compound eyes of all Crustaceans, led Beddard ('88, p. 447) to look for it in Serolis, he was not able to identify it. Watase ('90, pp. 290 and 293) was more fortunate, and succeeded in finding under each facet two cells in the corneal hypodermis. I have not been as successful as Watase was in determining the exact number of hypodermal cells in an ommatidium, but I have seen enough to convince me that such cells are present. In sections approximately tangential to the external face of the adult retina, one occasionally finds nuclei (Plate VI. Fig. 60, *nl. crn.*) between the distal ends of the cone cells and the corneal cuticula. These represent unquestionably the cells of the corneal hypodermis, and are not to be confused with the nuclei of the cone cells, which lie in a deeper plane. In making sections, the corneal cuticula splintered so irregularly that the tissue immediately below it was completely disarranged. It was therefore possible to get only irregular fragments of the tissue in this region, such as Figure 60 shows, and these fragments were always too small to admit of an accurate determination of the number of hypodermal cells under a single facet. I have also been equally unsuccessful in my attempts either to isolate these cells or to study them *in situ* on the corneal cuticula.

The eyes in the adult, owing to the thickness of the cuticula, are unfavorable for the study of the corneal hypodermis; but in embryos of even an advanced stage, the cuticula is so thin that the hypodermis can be studied with comparative ease. An ommatidium from the eye of an advanced embryo is seen in Figure 65; the ommatidium is viewed from the side. Distal to the cone (*con.*) four nuclei can be seen; one (*nl. crn. 1*) is superficial in position, three are deep. The relation of these nuclei to the ommatidium can be satisfactorily studied in sections transverse to the axis of the ommatidium. A series of three such sections is seen in Figures 66, 67, and 68. Of these, the most distal is that shown in Figure 66. This includes only the most superficial layer of the retina, and contains two nuclei (compare *nl. crn. 1*, in Figs. 65 and 66). These nuclei, as their position clearly indicates, represent cells of the corneal hypodermis. In the plane of the section which includes the three deeper nuclei of Figure 65, four nuclei are in reality present (Fig. 67); two of these (*nl. con.*) are large, and lie directly below the superficial ones in the corneal hypodermis; two are small (*nl. crn. 2*) and lie between the ends of the deeper large nuclei. Of the deep nuclei, the two large ones (*nl. con.*) rest one above each segment of the cone; in fact, as a section in a slightly deeper plane shows (Fig. 68, *nl. con.*), these nuclei coincide so closely with the segments of the cone that they must be regarded as the nuclei of the cone cells.

It is difficult to state what nuclei in the adult correspond to the smaller of the four deep ones in the embryo. The number of these nuclei (two) in the embryo equals the number of pigment cells which Watase ('90, p. 294) has described as surrounding the cone; but that these nuclei do not belong to such cells is evident from the fact that in the embryo, the nuclei of the pigment cells can be identified in a position somewhat proximal to that in which the smaller of the four nuclei occur (compare *nl. dst.* in Figs. 65 and 69.) Possibly the cells represented by these small nuclei in the embryo become in the adult the small interommatidial pigment cells, or it may be that they retain their relatively superficial positions, and, while occupying the space between the corneal facets, perhaps produce the cuticula of that region. In the fragments of the adult retina, from immediately below the corneal cuticula, small nuclei are not unfrequently met with in the spaces between the ommatidia. These are possibly derived from the smaller deep nuclei of the embryo.

It will thus be seen that my conclusions concerning the corneal hypodermis agree in the main with those of Watase; namely, that for each ommatidium there are two cells in this layer. Besides these, however, it is possible that the hypodermis may contain an equal number of other cells, which occupy positions immediately under the cuticula and between the ommatidia.

The facets in the *corneal cuticula* of Serolis, when viewed from the exterior, are irregularly circular in outline, often approaching a six-sided form. As I have already observed, they are arranged on the plan of the hexagonal type. The distal face of each facet is flat, or only slightly convex; the proximal face is decidedly convex. The curvatures of the two faces and the thickness of the cuticula in the facet of S. Schythei was about the same as that figured by Watase ('90, Plate XXIX. Fig. 1) for the species which he studied.

The *cone*, as Beddard ('84, p. 340) first demonstrated, and as Watase ('90, p. 290) afterwards confirmed, is composed of two nearly hemispherical segments, which correspond to the two cone cells. The protoplasmic material of each cone cell covers the curved surface of the segment to which it belongs, and contains a nucleus in its distal portion. These relations have been well shown by Watase ('90, Plate XXIX. Fig. 1).

From the condition presented even in advanced embryos (Fig. 65) it is evident that the part of the cone earliest formed, is the one which is nearest the applied faces of the two cone cells, and that from this as a centre the cone has continued to increase outwards. Although at this stage the outline of the cone itself is sharply marked (Fig. 65), the external limits of the cone cells are only approximately indicated by the distribution of the pigment granules, which have begun to form in the surrounding pigment cells.

In Serolis, as in Porcellio and Idotea, the cone cells and the cells of the corneal hypodermis are separated by the same perpendicular plane. There are some complications in the structure of the cone cells which can be discussed subsequently with greater clearness.

The *retinula* in Serolis, as Beddard ('84, p. 340) first observed, is peculiar in that it is composed of only *four* cells. My own observations add almost nothing that is new to the previous accounts of this structure. The figure which Watase has drawn ('90, Plate XXIX. Fig. 1) of the characteristic form of the retinular cell when viewed from the side and its relation to its rhabdomere, reproduces very closely the structural conditions which I have observed in S. Schythei.

The *rhabdome* in Serolis has been carefully studied by Beddard ('88, pp. 448–450). Owing to the complexity of its structure, one meets with difficulties in attempting to interpret its parts in terms of the relatively simple rhabdome of many Crustaceans. The peculiarities of this structure can be approached most satisfactorily perhaps from the side of its adult anatomy.

In a transverse section of the distal end of the rhabdome, five structures can be observed (Fig. 61). Four of these (Fig. 61, *rhb'm.*) are squarish pieces confluent on one side with a retinular cell, and in contact with one another only at their angles The sides of these pieces which are directed towards the axis of the ommatidium are convex, and together bound a central area which contains the fifth or axial structure (*cl. con.*). Each of the squarish pieces also exhibits a line slightly concave towards the axis of the ommatidium. This line, which might be taken for the separation between the axial and peripheral structures, is in reality entirely within the latter. That these are five separate structures is indicated by the fact, that in transverse section, when for any reason the elements have been broken apart, the separation almost always occurs on the lines which I have described as the limits of the different pieces.

Evidently the squarish masses (*rhb'm.*) on the axial faces of the retinular cell correspond to the rhabdomeres of other Crustaceans, and like these structures are produced by the cells to which they are attached. It is more difficult to explain the axial element, for it shows no indication of having been produced by the surrounding retinular cells, nor are there other cells in the neighborhood to which its production could be referred.

When the longitudinal extent of these structures is considered, the difficulty of explaining the axial portion is increased. In S. Schythei the rhabdomeres extend only a short distance distally and proximally, but throughout the whole of that distance they are closely applied to the axial face of the retinular cells. This condition has been well figured by Watase ('90, Plate XXIX. Fig. 1), and supports the statement already made that these bodies correspond to the rhabdomeres in other Crustaceans. I have never observed a rhabdomere, such as that figured by Beddard ('87, p. 234), in which the proximal half of the structure is not in contact with the retinular cell. The axial part has a much more considerable extent in a longitudinal direction than the rhabdomeres. Apparently it is continued proximally into a fibrous bundle which stretches towards the basement membrane, where according to Beddard ('88, p. 449) it may terminate as a single fibre.

From what has just been stated it must be evident that the so called rhabdome of Serolis consists of two sets of structures, one of which includes the four rhabdomeres and the other the axial part with its proximal fibrous prolongation.

The development of these structures has been studied by Beddard ('88, p. 450). In the youngest embryos which he examined, the axial portion was already formed, and at that stage it was closely invested by the four retinular cells and two other cells, the hyaline cells. Judging from their positions, Beddard believes that both kinds of cells may contribute to the formation of the axial structure, although the fact that this body is squarish in transverse section leads him to conclude that the four retinular cells play the more important part in its formation. Beddard regards the axial body as the rhabdome of the immature eye. In his opinion, the rhabdome in the adult is produced by subsequent secretions from the retinular cells, and presents the form of the four rhabdomeres already described. Although these rhabdomeres form the principal part of the rhabdome in the adult eye, he believes that the rhabdome of the earlier stages persists as the axial fibrous structure in the later stages, and constitutes perhaps the greater part of its distal continuation between the rhabdomeres.

Unless some such explanation of the origin of the axial part of the rhabdome as that proposed by Beddard be accepted, it is difficult to understand how the fibrous portion could arise as a secretion; for in the adult the proximal portion of it is touched by neither retinular nor hyaline cells.

Granting for the moment the adequacy of Beddard's explanation of the origin of the axial part, we are still confronted by what appears to me to be unparalleled in the structure of the eyes in Arthropods, namely, an ommatidium which produces two distinct rhabdomes. This may not be an impossibility, but if it occurs at all, it is certainly exceptional.

I believe, however, that the so called axial part of the rhabdome in Serolis is capable of another interpretation, against which the objections already suggested cannot be urged. That the axial portion terminates proximally on the basement membrane has been fairly well established by Beddard. The distal termination of it, however, has not been so clearly made out. It is my belief that the axial structure is directly continuous distally with the cone cells; in other words, that this structure is to be regarded as a proximal extension of the cone cells, not as a part of the rhabdome. The termination at the basement membrane of this prolongation of the cone cells, as observed by Beddard, is perfectly consistent with the interpretation which I have suggested, and makes the condition in Serolis similar to that in Homarus, where the fibrous ends of the cone cells also terminate on the basement membrane. That the fibrous structure should be present in the embryo of

Serolis before the formation of the rhabdome proper is rather in favor of my interpretation than opposed to it. The direct evidence that the axial body is a proximal extension of the cone cells is not as conclusive as could be desired. The condition which most favors this view is as follows. In longitudinal and transverse sections of the ommatidia, both in adult and embryonic specimens, no line of separation has been observed between the protoplasm at the deep end of the cone and the substance which occupies the axial part of the ommatidium proximal to the cone (compare Fig. 65). In attempting to determine the true relation, it is important to keep clearly in mind the fact that the proximal end of the cone, usually bounded by a sharply marked line, is *not* the proximal end of the cone cells ; but, as Watase ('90, Plate XXIX. Fig. 1) has well shown, the cone is surrounded proximally as well as laterally by the protoplasmic material of its cells. It is this material, not that of the cone proper, which forms the proximal elongation.

I had hoped that by isolating the elements of the retina I could obtain more conclusive evidence of the connection of these parts, but my efforts were of no avail. My ill success was due, I believe, not to any want of connection between the structures treated, but to the fact that the material at my disposal had been kept so long in strong alcohol that it had become unfit to serve for isolation. This conclusion seems to me to be confirmed by the fact that I was unable even to isolate satisfactorily the retinulæ, structures which are usually separable with ease in the fresh retinas of most Crustaceans.

If the view which I have set forth in the foregoing paragraphs concerning the interpretation to be put upon the axial part of the so called rhabdome of Serolis be correct, it follows that the true rhabdome of this Crustacean must be considered as composed of four rhabdomeres, each of which is applied to the axial face of its appropriate retinular cell, and that these four rhabdomes are prevented from uniting with one another by a proximal extension of the cone cells which occupies the axis of the ommatidium from the cone to the basement membrane.

Beddard ('84^a, p. 21), in his account of the eye in S. Schythei, states that the cone is "enclosed in a sheath of deep black pigment cells," and Watase ('90, p. 294) has observed that in this genus there are two such cells for each ommatidium. I believe that the number has been given correctly, for although I have not satisfactorily isolated the cells, I feel confident that I have identified their nuclei, and the number of these is twice that of the ommatidia.

The nuclei of these pigment cells are most satisfactorily seen in advanced embryos (compare *nl. dst.*, in Figs. 65 and 69). In transverse sections at this stage (Fig. 69) each cone is surrounded by a circle of six nuclei. Each nucleus, however, participates in three adjoining circles, consequently there are only twice as many nuclei as ommatidia. In the adult the nuclei of these pigment cells (Fig. 60, *nl. dst.*) occupy the same relative positions as in the embryo; in the latter, however, they are usually somewhat hidden by the pigment which surrounds them.

In the embryo the nuclei of the pigment cells surrounding the cone resemble very closely, except in point of size, the nuclei of the retinular cells (compare *nl. dst.* and *nl. px.* in Fig. 65). In the nuclei of the retinular cells there is usually one distinct nucleolus, sometimes two, but as a rule no finer particles. This condition also obtains in the nuclei of the pigment cells. Not only are the nuclei of these two kinds of cells similar in the embryo, but they are also much alike in the adult (compare *nl. dst.* in Fig. 60 with *nl. rtn.'* in Fig. 63).

Because of this resemblance, I believe that the pigment cells which surround the cone can be fairly considered to be modified retinular cells, which have lost their sensory function in precisely the same way as in the case of the distal retinular cells in Decapods (see Parker, '90^a, p. 57). If this interpretation of the pigment cells be accepted, it follows that in Serolis, as in Decapods, two kinds of retinular cells are present, proximal and distal, and that the primitive ommatidium from which that of Serolis was derived probably contained six retinular cells functional as nervous structures. It need scarcely be added, that this number is characteristic for the ommatidia of many Isopods.

The retinula in the species of Sphæroma which I studied presents an appearance which suggests the differentiation of simple retinular cells into proximal and distal cells. In Sphæroma there are seven retinular cells (Plate V. Fig. 58); three of these are considerably reduced; the remaining four are large, and recall the four retinular cells of Serolis. In transverse sections it can be shown that the four large cells in Sphæroma not only resemble in appearance the four proximal cells in Serolis, but that they occupy the same relative positions in the ommatidium. In Serolis the plane which separates the two cone cells of any given cone, when extended, separates the four proximal retinular cells into two groups of two cells each (compare Plate VI. Fig. 68 with Figs. 71 and 72). The plane of separation in the cone of Sphæroma divides the retinula by passing *through* the single small retinular cell shown in the lower part of Figure 58 (Plate V.) and *between* the two small cells on the opposite side, thus separating the four large retinular cells into two groups, as in Serolis.

The change which would convert an ommatidium like that in Sphæroma into one like that in Serolis is easily imagined. It would consist in the complete abortion of one of the three small retinular cells, and the conversion of the other two into the pigment cells surrounding the cone.

In addition to the elements which have already been described in the ommatidium of Serolis, there are certain small pigment cells which occur for the most part in the region of the retinulæ. Beddard ('84^a, p. 21) describes these as long branching "connective-tissue cells," a name which might imply that they originated from the mesoderm, and were therefore intrusive. Watase ('90, p. 293, Plate XXIX. Fig. 1) has also described and figured these cells, but distinctly states his belief that they are reduced ectodermic cells. In the adult I have observed in the region of the cones, as well as near the retinulæ, certain small nuclei which are usually surrounded with more or less black pigment. These, I believe, represent the cells described by Beddard and Watase. In the embryo certain scattered nuclei (*nl. h'drm.*, Figs. 65 and 70) occur in the spaces between the ommatidia. It is probable that these nuclei are ectodermic in origin, and I am at a loss to know what has become of them in the adult, unless they form the pigment cells already mentioned. I am therefore inclined to believe, with Watase, that the small additional pigment cells are reduced ectodermic cells.

The presence of the *hyaline* cells in the ommatidium of Serolis is, as Beddard has pointed out, almost a unique feature. These cells, usually two in each ommatidium, fill the space immediately below the rhabdome. They are bladder-like (Fig. 62, *cl. hyl.*) and contain each a large granular nucleus. Although it is stated that there are usually two of these cells in each ommatidium, I never found more than one to an ommatidium in the several eyes of S. Schythei which I examined. This circumstance, however, is not surprising; for, as Beddard ('84^a, p. 22) has remarked, the number of these cells is subject to variation, there being sometimes one, sometimes two, for each ommatidium. In S. Schythei the single hyaline cell envelops more or less completely the distal part of the fibrous portion of the cone cells, so that this part seems to pierce the hyaline cell. A closer inspection, however, will usually show two lines extending from the fibre to the periphery of the hyaline cell (compare Fig. 62), and these lines indicate, I believe, the two walls of the cell which have been infolded by the presence of the fibre during the growth of the hyaline cell.

The source of the hyaline cells is not definitely known. Their nuclei (Fig. 65, *nl. hyl.*), as Beddard ('88, p. 450) has observed, are present in the retinas of embryos; and, although the cells may possibly be intrusive, the evidence on the whole favors the view that they are ectodermic in origin.

Several functions have been attributed to the hyaline cells. Their close connection with what Beddard took to be the proximal extension of the rhabdome led him ('88, p. 450) to suspect that they might be rudimentary retinular cells, but, as he (p. 451) further remarks, the fact that no nerve fibres are connected with them opposes this view. Their transparency suggested to him ('84^a, p. 22) that they might form a part of the dioptric apparatus; but it is difficult to understand, considering their position, precisely what that function would be. I am inclined to believe, with Watase ('90, p. 293), that they are chiefly concerned with the support of the structures occupying the basal portion of the retina.

In the retina of S. Schythei many of the open spaces between the cones and the basement membrane contain free non-pigmented cells (Fig. 61, *cp. sng.*). These have a distinct nucleus, finely granular protoplasm, and a sharply marked outline. On account of the extreme variations in form which the different cells present, it is probable that when living they exhibited amœboid motion. In appearance they correspond exactly to the blood corpuscles of the body spaces, and as they occur not only in the retina, but also in the rather large openings through the basement membrane (compare Fig. 64), and in the space proximal to this membrane, I am of opinion that they are blood corpuscles.

The peculiarities which have led me to consider the ommatidium in Serolis separately from that of other Isopods, are two: the possession of one or more hyaline cells, and the presence of only four retinular cells. The latter peculiarity, as I have already shown, is not fully established; for in this genus, as in many other Isopods, the ommatidium really contains six cells, although two of these, the distal ones, are probably no longer functional as nervous structures. The other peculiarity, the possession of hyaline cells, is not a very important characteristic, for, as Beddard ('87, p. 235) has shown, these cells also occur in Ægа; and it is probable, moreover, that they must be regarded as abnormally enlarged elements, specialized from among those cells which in other Isopods fill the spaces between the ommatidia. What distinguishes the ommatidium in Serolis from that of other Isopods is, therefore, not so much the possession of hyaline cells as the fact that its retinular cells are differentiated into two sets, proximal and distal.

In accordance with the facts already presented, the number of cells contained in the ommatidium of Serolis can be stated as follows: cells of the corneal hypodermis, two, with possibly two others interommatidial in position; cone cells, two; retinular cells, six, two distal and four proximal; hyaline cells, one or two; a variable number of small pigment cells of ectodermic (?) origin.

Leptostraca.

The histological structure of the ommatidia in the Nebaliæ has been investigated, so far as I am aware, only by Claus ('88, pp. 65–84). I have had no material for the study of the eyes in these Crustaceans, and I can therefore only present, in the form of a summary, the more important results of Claus's exhaustive study.

In Nebalia there is a *corneal hypodermis* (Claus, '88, pp. 68 and 69), the cells of which are grouped in pairs. As in many of the higher Crustaceans, there is one pair of these cells for each ommatidium. The *corneal cuticula* is facetted; the outlines of the facets are circular, and adjoining facets are separated from one another by a small amount of intervening cuticula (Claus, '88, Taf. X. Fig. 10). The *cones* are composed of four segments (Claus, '88, p. 69). The structure of the *retinula* is somewhat complex. The greater part of the rhabdome is surrounded by seven retinular cells. Distal to these cells, however, are seven pigment cells, which enclose the proximal prolongation of the cone cells and the distal end of the rhabdome. Such a relation between pigment cells and retinular cells is not of common occurrence among Crustaceans, and it is possible that the bodies which Claus has taken for pigment cells are really the distal ends of the retinular cells. Claus describes and figures what he believes to be the nuclei of both kinds of cells, but I think his figures fail to show that these nuclei are within the limits of the cells to which they are said to belong. It seems to me quite possible that what he has described as two circles of seven cells each may be merely one circle seen at two different levels, as the correspondence in numbers suggests. This single circle would be of course composed of retinular cells, the nuclei of which are probably the distal ones of the two sets described by Claus. The proximal nuclei, which, according to Claus, belong to the retinular cells, occupy positions not unfrequently taken by the nuclei of accessory pigment cells, and I am inclined to think that such is their real nature. This interpretation would be more in accordance with the conditions found in ommatidia which have seven retinular cells than is the one given by Claus; but as I have not had the opportunity of studying the eyes in Nebalia, I can offer it merely by way of suggestion.

Probably two kinds of accessory cells are present in Nebalia; one of these extends from the corneal cuticula to the basement membrane, the other, the presence of which is not so fully established, probably occurs near the basement membrane.

Cumaceæ.

Excepting what is contained in Burmester's ('83, pp. 35–37) account of the degenerate eyes in Diastylis (Cuma) Rathkii, nothing, I believe, is known of the finer structure of the eyes in the Cumaceæ. The specimens at my disposal for the study of these eyes proved upon examination to be blind. At least, the optic plates of all the individuals which I examined, both when studied from the exterior and when examined in sections, showed no evidence of eyes. My material consisted of specimens of Diastylis quadrispinosa, G. O. Sars, and of three other undetermined species, two of which belonged to the genus Diastylis and one to Eudorella. These were kindly sent me by Prof. S. I. Smith.

Schizopoda.

The species of Schizopod the eyes of which I have studied is Mysis stenolepis, Smith. Specimens of this Crustacean were kindly collected for me at Wood's Holl, Mass., by Mr. C. B. Davenport. I am also under obligations to Dr. H. V. Wilson, of the United States Fish Commission, who at my request sent me specimens of this species freshly preserved in Müller's fluid.

In several of the previous accounts of the eye in Mysis the nuclei of the *corneal hypodermis*, although recognized, have been described as Semper's nuclei, i. e. as nuclei of the cone cells. The differences between the hypodermal nuclei and those of the cone cells can be easily seen in Mysis stenolepis (Plate VII. Fig. 73). In this species the hypodermal nuclei (*nl. crn.*) lie in a plane somewhat nearer the external surface of the eye than the nuclei of the cone cells (*nl. con.*). In transverse sections at the proper levels, each ommatidium will be seen to contain two elongated nuclei (Fig. 75, *nl. crn.*) belonging to the corneal hypodermis, and two oval nuclei (Fig. 76, *nl. con.*) in the cone. The hypodermal nuclei occupy such positions that the plane of separation between their cells would be at right angles to that between the cone cells (compare Figs. 75 and 76). The group of four nuclei, two belonging to the corneal hypodermis, and two to the cone cells, correspond without much doubt to the so called four Semper's nuclei mentioned by Claparède ('60, p. 194) in Mysis flexuosa, and described by Sars ('67, p. 33) in M. oculata. Nusbaum ('87, p. 179) also observed four similar nuclei in the developing eye of Mysis chameleo, and Grenacher ('79, p. 118) described the same number in Mysis vulgaris. In the last named species, according to Grenacher, the four nuclei are grouped in two pairs, one of which occupies a more distal plane in the ommatidium than the other. The more superficial pair undoubtedly belongs to the corneal hypodermis, the deeper pair to the cone cells.

It must be evident, then, that the nuclei of the cone cells and corneal hypodermis have not always been carefully distinguished. In all cases where they have been separated, the corneal hypodermis has been shown to possess two nuclei for each ommatidium.

The *corneal cuticula* in Mysis, as Frey and Leuckart ('47^a, p. 113) first pointed out, is facetted, and the outline of the facet is a circle. In Mysis stenolepis the circumference of the facet is tangential to the circumferences of six adjoining facets (Fig. 74). In Mysis vulgaris, Grenacher ('79, p. 118) has shown that the facet is not lens-like, but is of uniform thickness throughout. In M. stenolepis, however, the cuticula is often slightly thicker at the middle of the facet than at its edges (Fig. 73, *cta.*). In this respect, therefore, different species probably vary.

The *cones* in Mysis vulgaris, according to Grenacher ('79, p. 118), are composed of two segments. The same number is also present in the cones of M. stenolepis (compare Figs. 76–78, *con.*). In longitudinal sections the cone (Fig. 73, *con.*) appears to consist of a uniformly and finely granular substance enveloped in a delicate but distinct membrane. Near the distal end of the cone the material which composes it becomes more coarsely granular; in this the nucleus of the cone cell is usually lodged. Cones (Fig. 92) which have been isolated in macerating fluids are plumper and apparently not so contracted as those which have been subjected to the process of cutting. The nuclei also are rounder and fuller. The cone proper (Fig. 92 *con.*) occupies a more central position in the cone cells, and is surrounded by a finely granular material, which is especially abundant at the proximal end. The difference between the cone proper and this granular material was not generally observable in *sections* of the cones. In all of the many cones which I succeeded in isolating, the proximal ends invariably had a broken appearance. Consequently, I believe that I have never completely isolated a pair of cone cells. The question of the proximal extent of the cone I shall recur to later.

The *retinular cells* in Mysis are of two kinds, proximal and distal. The proximal cells extend from the basement membrane distally to the level at which the cone rapidly contracts. The pigment which they contain is for the most part concentrated around the rhabdome, and their nuclei occupy a distal position in the cell (Fig. 73, *nl. px.*).

In Mysis the number of cells comprising the retinula is at least seven (Figs. 85–87). Possibly, as I have elsewhere suggested (Parker, '90^a, p. 55), the total number of cells in this retinula, as in that of Homarus, may be eight.

In order to determine this question, I have counted the number of nuclei in several retinulæ of Mysis. The enumeration of these can be easily followed in Figures 79 to 82. These figures represent successive transverse sections through four ommatidia, in the region occupied by the proximal retinular nuclei. The axis of each ommatidium is marked by the fibrous portion of the cone cells (*cl. con.*), and the same ommatidium is designated in different sections by the same Roman numeral. The nuclei in ommatidium II. can be counted the most readily. In Figure 79, which represents the most distal section of the series, the cone in ommatidium II. is surrounded by a circle of six nuclei, which have been numbered from 1 to 6. Each of these nuclei, however, participates in three circles (compare nucleus 5), and hence only two of the six can be referred to ommatidium II. Two similar circles occur, one in the sections shown in Figure 80, and one in that shown in Figure 81. As in the former instance, two nuclei in each circle belong to ommatidium II. In these three circles, then, there are in all six nuclei to be allotted to ommatidium II. In addition to these nuclei, it will be noticed that to the right of the cone in Figure 80 there is one more nucleus (No. 7), and still another in a similar position in Figure 82. These two nuclei, when added to the six already summed up for ommatidium II., make a total of eight nuclei for this ommatidium.

The same number of nuclei occurs in each of the other three ommatidia, but their arrangement is not quite so regular as in the one just counted. From this I conclude that the number of nuclei in a retinula of Mysis is eight.

The different nuclei in this retinula usually present a very uniform appearance. The most proximal one differs somewhat from the others in being more elongated (compare Figs. 73 and 82). The seven distal nuclei, on account of their general resemblance, belong, I believe, to the seven functional retinular cells. The single proximal nucleus probably represents an eighth rudimentary cell. The position of this nucleus, proximal to the other retinular nuclei, is similar to that occupied by the nucleus of the rudimentary retinular cell in Homarus (compare Parker, '90^a, pp. 20, 21).

The *rhabdome* in Mysis stenolepis lies in the proximal portion of the retina. It is rather stout, blunt at its distal end, but sharper proximally (Fig. 90). Its surface is marked with coarse corrugations. In transverse section, its outline is a square; this is subdivided by two lines into four smaller squares, a condition already observed by Grenacher ('79, p. 119) in M. flexuosa. The relation of the retinular cells to these divisions of the rhabdome can be clearly seen in Figure 87.

According to Grenacher's account ('79, p. 118), a rod-like structure extends, in Mysis vulgaris and M. flexuosa, through the axis of the ommatidium from the distal end of the rhabdome to the region of the proximal retinular nuclei. Whether this rod be a proximal continuation of the cone, or a distal extension of the rhabdome, Grenacher found it difficult to decide. He is inclined, however, to the former opinion.

A similar structure occurs in the ommatidia of Mysis stenolepis. Although I have made repeated attempts, I have never succeeded in isolating the rod in connection with either the rhabdome or the cone cells. In transverse sections, the distal end of it appears in a position slightly proximal to the retinular nuclei (Figs. 73 and 83). The cone cells extend proximally as a transparent axis to this region, and the most distal indications of the rod are four fibres which lie on the periphery of what I take to be the proximal end of the cone cells (Fig. 83). Somewhat deeper than this, the four fibres thicken, and finally fuse (Fig. 84), producing a body which in transverse section has the outline of a four-pointed star. In a plane slightly more proximal, the outline changes to a squarish one (Fig. 85), and this is retained almost to the proximal end of the rod. Throughout its extent, this problematic rod is closely surrounded by the seven proximal retinular cells (Fig. 85). It is separated from the rhabdome by what appears to be an open space (Fig. 90, at the level of the dotted line 86). In transverse sections (Fig. 86), however, this space is seen to be divided by delicate membranes into four compartments.

These facts, however, do not aid much in deciding the relationship of the rod. The fact that it shows indications of being composed of four parts suggests its connection with the rhabdome. The four parts of which it consists do not, however, correspond in position to the segments of the rhabdome, but fall between them. (Compare Figs. 83 and 87.) On the other hand, if it were an extension of the cone, one would expect it to be composed of two, instead of four parts. Its position, however, is one which is more frequently occupied in other Crustaceans by a slender extension of the cone cells than by a process from the rhabdome, and, notwithstanding its division into four parts, I am inclined to agree with Grenacher, and to regard it as belonging to the cone cells rather than the rhabdome.

The distal retinular cells in Mysis surround the lateral faces of the cones (Fig. 73, *cl. dst.*). Apparently they reach the cuticula; their proximal ends are attenuated and become lost in the region of the nuclei of the proximal cells. Their pigment is limited to their proximal halves, and consists of a distal layer of brownish material, proximal to which is a much more extensive deposit of blackish granules. Each cone is surrounded by six of these cells, as can be seen from their outlines (Fig. 78, *cl. dst.*), and still more satisfactorily from the arrangement of their nuclei (Fig. 75, *nl. dst.*). Each cell, however, participates in three circles; consequently, there are only twice as many of these cells as ommatidia.

The axis of each distal retinular cell is occupied by a transparent rod, which in transverse section has the appearance of a light spot (Fig. 77). In depigmented sections stained with Kleinenberg's hæmatoxylin, these rods are deeply colored (Fig. 78). I shall recur to their probable significance.

The pigment which is found in the region of the rhabdomes in Mysis is of two kinds: blackish granules, and a fine flaky material, white by reflected light, yellowish by transmitted light. The black granules are for the most part contained in the retinular cells. The lighter pigment is always associated with certain nuclei, two of which are shown in Figure 90 (*nl. ms'drm.*). These nuclei are closely invested by the pigment, and probably belong to the cells in which the pigment is contained.

The source of the yellowish pigment cells is not easily determined. Apparently they are not limited to the retina, but also occur in the spaces below it. At least these spaces contain masses of pigment and nuclei which in all essential respects are similar to those distal to the membrane (compare the two nuclei, *nl. ms'drm.*, Fig. 90). In one case the nucleus of one of these cells was found apparently caught in its passage through an opening in the basement membrane (Fig. 91). For these reasons I believe that the yellowish pigment cells on the two sides of the membrane have had the same origin. The question as to the source of the yellowish pigment cells in the retina, therefore, appears to me to involve that of the origin of the similar cells beneath the retina. If I am right in this conclusion, all these cells must either have arisen in the retina, many of them migrating in a proximal direction out of it, or they must have had some extra-retinal origin, some of them migrating into it. On account of the considerable numbers in which they exist in the spaces below the retina, it seems to me much more probable that they have had an extra-retinal origin than that they have come from the retina itself. If this is their source, it is evident that those which are in the retina are intrusive. The nucleus which has already been mentioned as caught in an opening of the basement membrane (Fig. 91) has more the appearance of a body which is making its way into the retina than of one which is moving in the reverse direction, and may therefore be regarded as confirming to some extent the view of the extra-retinal origin of these cells. Their source, however, cannot be stated with certainty. Their power of migration implies amœboid activity, and this might be taken as an indication of their mesodermic origin.

The following cells characterize the ommatidium of Mysis: cells of the corneal hypodermis, two: cone cells, two; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory pigment cells (mesodermic ?) present.

Stomatopoda.

The material which I have had for the study of the eyes in the Stomatopods consisted of two specimens of Gonodactylus chirarga, Latr. These were kindly given me by Mr. W. S. Wadsworth, who had collected them in the Bermudas. One of them had been killed in hot water and preserved in alcohol; the other was both killed and preserved in strong alcohol; both were in excellent histological condition.

In Gonodactylus, as I have previously mentioned, there are two kinds of ommatidia; these differ in no important respect except size.

Longitudinal sections of both kinds are represented on Plate VIII.; the figure of the larger kind (Fig. 94) is taken from a depigmented section, that of the smaller one (Fig. 95) from a section containing the pigment in its natural condition. In the following description I shall give an account of the structure of the larger ommatidia, alluding to the condition of the smaller ones only when it differs in some important respect from that of the others.

The *corneal hypodermis* is represented in the ommatidium of Gonodactylus by two cells, the nuclei (Figs. 94–96, *nl. crn.*) of which can be recognized easily. Directly under the corneal cuticula each pair of hypodermal cells is in contact with similar pairs belonging to adjoining ommatidia, so that the layer here forms a continuous sheet. In a more proximal plane the neighboring pairs of hypodermal cells are not in contact (compare Fig. 93, a tangential section in which the extreme right-hand edge represents the condition immediately below the cuticula, while the parts to the left represent central portions successively more proximal in position). The only indication of a separation between the two hypodermal cells of each pair is seen in the distal projection of the cone between the two hypodermal nuclei (compare Figs. 94 and 96, *con.*).

The *corneal cuticula* in Gonodactylus is facetted, but the proximal and distal faces of the facets are apparently plane. Over the smaller ommatidia the facets are hexagonal in outline, whereas over the larger ones they are rectangular, and their arrangement is often indicative of the tetragonal system. In Squilla mantis, according to Will ('40, p. 7), the facets are hexagonal.

The *cones* in Gonodactylus are composed for the most part of a uniformly granular substance. Distally, they are pointed and probably touch the corneal cuticula; proximally, they terminate at the rounded end of the rhabdome (Fig. 94). Each cone contains in its distal enlargement four nuclei (Fig. 97, *nl. con.*), two of which lie directly proximal to the nuclei of the corneal hypodermis, while the remaining two alternate with them (compare Figs. 96 and 97). The proximal part of the cone is divided longitudinally into four segments (Fig. 98). Each segment, if extended distally, would include one of the four nuclei, and corresponds to one of the four cells by which the cone was produced. In Squilla mantis, according to Steinlin ('68, p. 17), the cone is also composed of four segments.

The *retinular cells* of Gonodactylus are of two kinds, proximal and distal. The proximal cells, constituting the retinula itself, surround the rhabdome completely, and extend distally only a short distance beyond it (Fig. 95). They contain only a small amount of pigment, which is concentrated in two regions, at their distal ends and near the basement membrane. The rhabdome is surrounded throughout its length by a thin but rather dense layer of pigment. This layer is more extensive in the smaller ommatidia (Fig. 102) than in the larger ones. The nuclei of the proximal retinular cells (Figs. 94 and 95, *nl. px.*) are located near their distal ends.

The number of cells in the retinula of Squilla, as described by Grenacher ('77, p. 33) and by Hickson ('85, p. 341, Fig. 2), is seven. In

Gonodactylus (Fig. 101) the retinular cells are certainly as numerous as in Squilla; but seven obvious cells in the retinula, as I have already shown in Mysis, may suggest the presence of eight in all, one of them being rudimentary. This condition is in fact characteristic of Gonodactylus also, as can be seen in the series of ommatidia shown in Fig. 100. These six ommatidia represent consecutive individuals in one of the bands of larger ommatidia previously mentioned. The band as a whole is cut obliquely, and in such a way that the ommatidia from 1 to 6 are cut successively in deeper or more proximal planes. In ommatidium 1 the rhabdome is surrounded by seven retinular cells, four of which are upon the right side and three upon the left. In addition to these, a large nucleus (*nl. px.*) lies close to the rhabdome. Ommatidium 2 has essentially the same structure as ommatidium 1. In ommatidium 3 the nucleus corresponding to the one seen in ommatidium 1 and 2 is no longer visible, but in its stead there is a small mass of granular protoplasm. A similar mass is also seen in ommatidia 5 and 6. It is usually present directly proximal to the nucleus figured in ommatidia 1 and 2, and is, I believe, the protoplasmic body of the cell to which this nucleus belongs. In ommatidium 4, the seven nuclei of the seven large (functional) retinular cells can be seen. These nuclei appear very large in transverse section compared with the cells in which they occur. It is probable that the cell wall is distended by them, although, owing to the indistinctness of the cell boundaries, I have not obtained positive evidence of this. In ommatidium 6 the seven retinular cells are seen in section at a plane proximal to that in which their nuclei lie. As in ommatidium 1, three of them are upon one side of the rhabdome and four upon the other. In a part of the ommatidium more proximal than that shown in number 6 (Fig. 100), the transverse section of the retinula has the appearance seen in Figure 101. Here the retinular cells have the same relation to the rhabdome that they do in ommatidium 6 (Fig. 100), except in the case of the upper right-hand cell of that figure. This cell enlarges in its more proximal portion, and comes to occupy a position directly below the cell whose nucleus is shown in ommatidium 1 (Fig. 100). The gradual disappearance of this distal cell as one proceeds in a proximal direction from the plane of number 6, Figure 100, to that of Figure 101, and the gradual shifting in the position of the cell which replaces it proximally, can be followed so easily that there is not the least question as to the accuracy of the relations described. It is evident, then, that in Gonodactylus, as in Mysis, the retinula consists of eight cells, one of which is rudimentary.

The *rhabdome* (Figs. 94 and 95, *rhb.*) in Gonodactylus is an elongated rod-like structure of uniform thickness, which extends from the region of the proximal retinular nuclei to the basement membrane. It shows a distinctly toothed edge (Fig. 94), especially in specimens which have been treated with potassic hydrate. In transverse section it is squarish. Owing to its small size, the exact relation of the seven surrounding cells to its four faces cannot be easily determined. The single unpaired cell (Fig. 101) certainly lies opposite a face, not an angle. In this respect it agrees with the unpaired cell in Squilla as figured by Grenacher ('79, Taf. XI. Fig. 122). Probably in Gonodactylus the remaining six cells are related to the sides of the rhabdome as the corresponding ones are in Squilla (compare Grenacher's Fig. 122). In Gonodactylus the retinular cells and rhabdome are in close contact with one another. The separation of these elements as figured by Grenacher in Squilla is probably artificial, as Grenacher himself suggests. In Squilla, according to both Steinlin ('68, p. 17) and Grenacher ('79, p. 125), the rhabdome in transverse sections is subdivided into four equal parts, somewhat as in Mysis. I have not observed this condition in Gonodactylus.

The *distal retinular cells* in Gonodactylus occupy the usual position near the cones. They contain very little pigment, and their number can be determined only by that of their nuclei. These agree with the nuclei of the proximal cells in the possession of a single well defined nucleolus, which is most readily seen in depigmented sections (compare *nl. dst.* and *nl. px.* in Fig. 94). The distal nuclei, especially in the region of the larger ommatidia, are arranged in rows which alternate with the rows of cones (Fig. 99, *nl. dst.*). Although the nuclei are not very definitely arranged, they often show a tendency to be grouped in pairs, and these pairs are so placed that in each row there is evidently one for each adjacent ommatidium. Moreover, in equal lengths of adjoining rows of nuclei and cones, the nuclei are always double the number of cones. I am convinced by these facts that there are two distal retinular cells for each ommatidium.

Besides the cells already described, certain others occur in the proximal part of the retina in Gonodactylus. These are represented by a few small, elongated nuclei (Fig. 94, *nl. ms'drm.*), which are very similar in appearance to certain nuclei occurring in the spaces below the basement membrane. I therefore believe that in Gonodactylus, as in Mysis, the proximal portion of the retina is occupied by intrusive cells, which are probably mesodermic in origin.

The kinds of cells found in the ommatidium of Stomatopods are as follows: cells of the corneal hypodermis, two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells (mesodermic?) present.

Decapoda.

I have studied the eyes of the following species of Decapods: Gelasimus pugilator, Latr.; Cardisoma Guanhumi, Latr.; Cancer irroratus, Say; Hippa talpoida, Say; Palinurus Argus, Latr.; Pagurus longicarpus, Say; Homarus americanus, Edw.; Cambarus Bartonii, Fabr; Crangon vulgaris, Fabr.; and Palæmonetes vulgaris, Say. I collected much of this material at the Station of the United States Fish Commission at Wood's Holl, Mass. The specimens of Cambarus were obtained in the vicinity of Philadelphia. I am under obligations to Mr. Herbert M. Richards for specimens of Palæmonetes collected by him at Newport, R. I. A number of eyes of two Crustaceans, Cardisoma and Palinurus, were kindly obtained for me by Mr. Isaac Holden; they were collected on the coast of Florida by Mr. Ralph Munroe, to whom I am indebted for the careful way in which they were preserved.

The *corneal hypodermis* in Decapods was first recognized by Patten ('86, pp. 626 and 642), who observed it in Penæus, Palæmon, Pagurus, and Galathea. Since Patten's announcement of the presence of this layer in Decapods, it has been identified in a number of other genera: in Crangon by Kingsley ('86, p. 863), in Alpheus by Herrick ('86, p. 43), in Astacus by Carrière ('89, p. 225), in Cambarus and Callinectes by Watase ('90, pp. 297 and 299), and in Homarus by myself ('90^a, p. 6). More recently I have observed it also in Palæmonetes (Plate IX. Fig. 103, *cl. crn.*), Crangon, Cambarus, Palinurus, Pagurus, Hippa, Cancer, and Cardisoma.

In almost all Decapods in which the arrangement of the cells in the corneal hypodermis has been observed, these elements have been found to be grouped in pairs, and so distributed that each pair occupies the distal end of an ommatidium (compare Figs. 103 and 106, Plate IX.). This arrangement has been observed, either by others or by myself, in the genera mentioned in the preceding paragraph, except Callinectes, in which the exact arrangement of the cells has not been recorded. Reichenbach's statement ('86, p. 91), that in Astacus there are four hypodermal cells under each facet, is probably erroneous, as Carrière's observations show.

Although Patten was the first investigator who clearly demonstrated the presence of the corneal hypodermis in Decapods, Grenacher, in 1879, described, I believe, the nuclei of this layer, without however correctly interpreting them. In his account of the ommatidium in Palæmon, Grenacher ('79, p. 123) mentions two kinds of bodies in what he takes to be the distal ends of the cone cells. Of these, the more distal ones (Taf. XI. Fig. 117, *n.*) represent, in his opinion, the nuclei of the cone cells; the more proximal (Fig. 117, Kk^1.) he considers as differentiated parts of the cone itself. The positions occupied by these bodies in Palæmon, and by certain bodies which I have observed in Palæmonetes (Plate IX. Fig. 103), are so similar that I believe the structures in the two genera to be homologous. In Palæmonetes the distal bodies lie in the cells of the corneal hypodermis (Fig. 103 *cl. crn.*), and are the nuclei of these cells. They represent what Grenacher considered the nuclei of the cone cells in Palæmon. The proximal bodies in Palæmonetes (Fig. 103, *nl. con.*) are unquestionably the nuclei of the cone cells, yet they correspond to what Grenacher considered the four pieces of the distal segment of the cone. I therefore believe that what Grenacher has described as the nuclei of the cone cells are really the nuclei of the corneal hypodermis, and that what he considered distal segments of the cone are the nuclei of the cone cells.

The *corneal cuticula* in Decapods, in correspondence with the differentiated condition of the corneal hypodermis, is facetted. The outline of the facets is either hexagonal or square. The particular genera in which these different kinds of facets occur have already been mentioned in dealing with the arrangement of the ommatidia in Decapods. The faces of the facets in Decapods are usually very nearly plane, but in Palæmon according to Grenacher ('79, p. 123), and in Palæmonetes (Plate IX. Fig. 103, *crn.*) according to my own observations, the facets are slightly biconvex. In Homarus, as Newton ('73, p. 327) has observed, and in Astacus according to Carrière ('85, p. 167), the distal surface of the facet is plane, the proximal slightly convex. In even the most extreme cases, however, the convexity of the facets in Decapods is not sufficient to make them very effective as lenses.

The facets in Decapods are generally bisected by a fine straight line. This line, as Patten has suggested, probably represents the plane of separation between the two subjacent hypodermal cells. In the square facets this line either divides the facet diagonally, as in Homarus (Parker, '90^a, Fig. 2), or transversely, as in Palæmonetes (Plate IX. Fig. 105). In the hexagonal facets it either bisects opposite sides, as in Cancer (Plate X. Fig. 126), or unites opposite angles, as occasionally in Galathea (Patten, '86, p. 644, Plate 31, Fig. 114). Leydig's ('57, p. 252, Fig. 134) figure of Astacus, in which each facet is subdivided by *two* diagonal lines into four areas, and Newton's ('73, p. 327) statement that the same condition occurs in Homarus, are probably incorrect.

The *cones* in Decapods are composed of four segments. This number was first observed by Will ('40, p. 13) in Palæmon, and has since been recorded in many other genera. So far as I am aware, there are no Decapods in which the number of segments is not four. As Claparède ('60, p. 194) first pointed out in Galathea and Pagurus, each segment contains a nucleus and represents a single cell. Although the significance of these nuclei was without doubt first fully appreciated by Claparède, it is probable that they were previously seen by Leydig ('55, Taf. XVII. Fig. 31) in the crayfish.

As a rule, the distal termination of the cone cells is on the proximal side of the corneal hypodermis. In the lobster, however, and in Palæmonetes (Plate IX. Fig. 104), the pointed ends of these cells pass between the two cells of the corneal hypodermis, and probably come in contact with the corneal cuticula near the middle of a facet.

It is difficult to determine with accuracy the proximal termination of the cone cells. They can be easily traced to a region immediately distal to the distal end of the rhabdome. In this region, as Schultze ('68, Taf. I. Figs. 9 and 11) has clearly demonstrated in Astacus, the fibrous ends of the four cone cells separate, and pass partially around the rhabdome. In Homarus, these fibres extend proximally, and finally terminate at the basement membrane. A similar method of termination also occurs in Palinurus. In the other genera which I have studied, the fibres, although visible near the distal end of the rhabdome, are lost in the adjacent tissue, and I do not know whether they terminate in this tissue without special attachment, or whether they make their way as excessively fine fibres to the basement membrane. The separation of the fibrous ends of the cone cells, near the distal end of the rhabdome, has been observed by Steinlin ('66, p. 93) in Palæmon, and by Schultze ('67 and '68) in several other Decapods. The statement made by many of the older investigators, and recently reaffirmed by Patten, that the cone and rhabdome are parts of one continuous structure, is without doubt incorrect.

The resolution of the *retinula* into its cellular constituents was first attempted in Decapods by Leydig ('55, p. 408), according to whom the retinula of Herbstia contains four cellular bodies, the nuclei of which can be distinguished in the distal part of the structure. A somewhat similar condition was described by Newton ('73, p. 333) for Homarus;

in this genus, as in Herbstia, it was maintained that there were only four cells. Subsequent investigators have not confirmed this conclusion. In transverse sections of the retinula of Palæmon, Grenacher ('77, p. 32) has demonstrated that the rhabdome is surrounded by *seven* retinular cells. He also ('77, p. 33, and '79, p. 125) observed the same number in the retinulæ of Astacus and Portunus. Since the publication of Grenacher's observations, a retinula containing seven cells has been seen in Astacus by Carrière ('85, p. 169), in Penæus, Palæmon, Galathea, and Pagurus by Patten ('86, pp. 630 and 643), and in Cambarus by Watase ('90, p. 299).

In Homarus, as I ('90^a, p. 21) have already shown, the retinula contains, in addition to the seven functional retinular cells, an eighth rudimentary one, which is little more than a nucleus. In order to ascertain the presence or absence of this eighth cell in other Decapods, I have been careful to record the number of retinular nuclei, as well as the number of functional retinular cells. In some genera, such as Cardisoma and Hippa, I have not been able, on account of the unfavorable condition of the tissue, to make this determination; but in Palæmonetes, Palinurus, Cambarus, Crangon, and Cancer, I have succeeded in ascertaining the number both of the functional cells and of the nuclei in the retinulæ.

In Palæmonetes each rhabdome is surrounded by at least seven retinular cells (Plate IX. Fig. 114, *cl. px.*). The nuclei of these cells usually lie slightly distal to the rhabdome (Fig. 104, *nl. px.*). Their arrangement is shown in Figures 110, 111, and 112, which represent a series of consecutive sections through the region occupied by the proximal retinular nuclei of five ommatidia. The nuclei of the different ommatidia are arranged upon the same plan, and the corresponding nuclei in the different sets have been marked by the same number. In several instances, nuclei have been cut in two, and their parts are found in consecutive sections; in such cases the separate portions have been marked with the same number. As can be seen in these figures, the number of nuclei in the distal portion of each retinula is seven. But in addition to these, there is also another one, which occupies a position near the rhabdome. This nucleus resembles the others in all respects except that it is somewhat longer and narrower. It is drawn in Figure 103 at the level marked 114, and in Figure 114 one can see the regularity with which it occurs. This nucleus is the eighth in the retinula of Palæmonetes, and since it differs somewhat in structure from the other seven, and occupies a more proximal position, I believe it represents a rudimentary retinular cell.

In the distal portion of the retinula in Cambarus there are eight nuclei. The arrangement of these, as seen in successive transverse sections, is shown in Plate X. Figs. 118 to 122. In Figure 118, which represents the most distal section of the series, there are four nuclei, and these are so arranged that there is evidently one for each ommatidium.[1] In the next section (Fig. 119) there are seven nuclei, none of which were seen in Figure 118 ; the place for an eighth is indicated by an open area, and the eighth nucleus itself is seen somewhat out of place in Figure 120 (x). Four of the eight nuclei belonging in Figure 119 are arranged in a manner similar to those in the preceding section, but are not to be confounded with them. The remaining four are so placed that there are two for each ommatidium. Hence in this plane there are, as a whole, three times as many nuclei as there are ommatidia. In the next section (Fig. 120), omitting the nucleus marked x, which has been recorded as belonging to the preceding section, there are four nuclei, so arranged that there is one for each ommatidium. In the following section (Fig. 121) the nuclei, omitting the one marked x, which will be considered as belonging to the next following section, are so arranged that there are two for each ommatidium. In the last section (Fig. 122), the nuclei are not so regularly grouped as in the previous section, but when taken with the nucleus marked x in Figure 121, they constitute a group of four, the arrangement in which is such that each nucleus is intermediate between *four* groups of cone cells rather than between *two*, and therefore in the plane of this section there is one nucleus for each ommatidium. From this enumeration it is evident that the total number of retinular nuclei is eight ; namely, one in the first section, three in the second, one in the third, two in the fourth, and one in the fifth. The structure of these nuclei affords no clue as to which one belongs to the rudimentary cell.

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[1] The nuclei shown in Figures 118 to 122 are arranged upon either the plan shown in Figure 118 or that in Figure 121 (omitting nucleus x). Imagine the arrangement in Figure 118 extended over a large surface. The groups of four cone cells could then be regarded as forming lines in the direction of the length of the plate. These lines would alternate with lines of nuclei, and as the nuclei in any line would alternate with the groups of cone cells in an adjoining line, the number of nuclei must equal exactly the number of groups of cone cells ; i. e. in this arrangement there is one nucleus for each ommatidium. In a similar way, alternating vertical lines may be constructed from the arrangement in Figure 121. One line would be composed entirely of nuclei situated one opposite each group of cone cells ; the other, of alternating nuclei and groups of cone cells. In the former, as well as in the latter, there would be as many nuclei as groups of cone cells. Hence, in this arrangement the nuclei are twice as numerous as the groups of cone cells ; i. e. there are two nuclei for each ommatidium.

In Palinurus (Plate X. Fig. 125, *nl. px.*), the eighth nucleus is regularly present and easily seen. In Cancer (Fig. 129, *nl. px. 8*) it occupies a position between the adjacent retinulæ. It can also be identified in Crangon.

The retinulæ in Decapods, according to all recent observers, contain seven functional cells. In Homarus, Palinurus, Cambarus, Crangon, Palæmonetes, and Cancer, the retinulæ contain, in addition to the seven nuclei of the functional cells, an eighth nucleus, which represents, I believe, a rudimentary cell. It is probable, therefore, that in all Decapods each retinula really contains eight cells, one of which is rudimentary.

The *rhabdome* in Decapods presents a very uniform structure. It is usually an elongated body, pointed both at its distal and its proximal end, and completely covered, except at its distal tip, by the proximal retinular cells. In those Decapods in which it is large enough to be conveniently observed, its transverse section is squarish, and usually subdivided by two straight lines into four smaller squares (Plate IX. Fig. 113). As Grenacher ('77, pp. 31, 32) first demonstrated in Palæmon, the retinular cells are rather peculiarly arranged around the rhabdome. One of its four sides is flanked by *one* cell, the other three by two cells each. This arrangement can be seen in Palæmonetes (Fig. 113), and probably obtains for all Decapods.

In Palinurus Argus (Plate X. Fig. 124) there appears to be no rhabdome, unless the translucent axial portion of each retinular cell can be said to represent segments of it. The fibrous ends of the cone cells (*cl. con.*) can be easily identified between the retinular cells, but the centre of the retinula is filled with pigment, and shows not the least trace of a rhabdome. This peculiarity of Palinurus was noticed as early as 1840 by Will ('40, p. 15), who described the ommatidium in this genus as being without a transparent mass (= rhabdome).

Although the *distal retinular* cells in Decapods were collectively recognized by Müller ('26, pp. 355, 356) some sixty years ago as a definite pigment band in the distal portion of the retina in the crayfish, they were not identified as separate cells until quite recently. The first investigator to observe them was Carrière ('85, p. 169), who described them in Astacus as a pair of pigment cells flanking each cone. In Cambarus, Crangon, and Homarus, they also cover the sides of the cone, and in the last named genus they are produced proximally into long fibres, which perhaps pass through the basement membrane. In Palæmonetes (Plate IX. Fig. 108, *cl. dst.*) and in Cancer (Plate X. Fig. 127, *cl. dst.*) they are reduced to pigmented threads, which, starting from comparatively large bases, twine around the lateral surfaces of the cones.

The arrangement and number of the distal retinular cells can be most readily determined from their nuclei. In Cancer (Plate X. Fig. 128) the cells are arranged in circles of six around each group of cone cells; each cell, however, participates in three circles, and consequently there are in reality only twice as many cells as ommatidia. This arrangement of the cells also occurs in Cardisoma, Hippa, and Pagurus. In Crangon (Fig. 123), as I have previously remarked, the nuclei of the distal retinular cells are arranged in rows alternating with the rows of cones. There are twice as many nuclei as cones; hence I conclude that here also there are two distal cells for each ommatidium. In Homarus, Palinurus, Cambarus, and Palæmonetes (Plate IX. Figs. 103 and 109, *nl. dst.*) the nuclei are grouped distinctly in pairs, one pair for each ommatidium.

Each cone in Penæus, according to Patten ('86, p. 634), is surrounded by two pairs of pigment cells, and Watase ('90, p. 299) states that in Cambarus the dioptric part of the ommatidium is sheathed by *four* pigment cells. In Cambarus Bartonii I have been able to find only two such elements, the pair of distal retinular cells already described, and in the other Crustaceans which I have studied I have observed nothing which supports Patten's statement concerning the four pigment cells in Penæus. I am therefore inclined to doubt the accuracy of these two observations.

The interommatidial space in the basal part of the retina in Palæmonetes contains a light pigment similar to that described in the retina of Mysis. Like this the pigment in Palæmonetes is white by reflected light, and yellowish by transmitted light (compare Plate IX. Fig. 115). It is apparently contained within cells (Fig. 103, *cl. ms'drm.*) whose outlines are very irregular, and whose nuclei (Fig. 104, *nl. ms'drm.*) are small and somewhat variable in form. These cells occur on both sides of the basement membrane. As in Mysis, they have probably migrated into the retina, and are perhaps mesodermic in origin. They have been seen by Carrière ('85, p. 169) in Astacus, by Patten ('86, p. 636) in Penæus, and by myself ('90^a, p. 25) in Homarus. I have also recently observed them in Crangon, Cambarus, Cardisoma, Pagurus, and Palinurus, as well as in Palæmonetes.

From what has preceded it is evident that the ommatidium in Decapods contains the following elements: cells of the corneal hypodermis, two; cone cells, four; proximal retinular cells, eight, one of which is rudimentary; distal retinular cells, two; accessory cells, mesodermic (?) in origin, often present.

TABLE OF OMMATIDIAL FORMULÆ.

I have now concluded my account of the structure of the ommatidia in Crustaceans, and for the purpose of presenting in a condensed form its more important features I have devised the following table. This consists of a series of ommatidial formulæ constructed upon the plan which I have described in the Introduction. The figures indicate the numbers of particular kinds of cells present in the ommatidium of a given group. The abbreviation *pr.* (present) marks the presence of any kind of cell when the number of that kind is not constant for different ommatidia in the same individual.

TABLE SHOWING THE CELLULAR COMPOSITION OF THE OMMATIDIAN CRUSTACEANS.

Groups of Crustaceans.	Cells of Corneal Hypodermis.	Cone Cells.	Retinular Cells.			Accessory Cells.
			Undifferentiated.	Differentiated.		
				Proximal.	Distal.	
Amphipoda,	pr.	2	5			pr. (ect. ?)
Branchiopodidæ and Apusidæ,	2	4	5			0
Estheridæ,	pr.	5 (4)	5			0
Cladocera,	?	5	5			pr. (ect. ?)
Copepoda: Pontella,	pr.	2	5			pr. (ect. ?)
Sapphirina,	?	?	3			?
Argulus,	pr.	4	5			?
Isopoda: Idotea,	2	2	6			pr. (ect. ?)
Porcellio,	2	2	7			pr. (ect. ?)
Serolis,	2 (+?)	2		4	2	pr. (ect. ?)
Nebaliæ,	2	4	7			pr. (ect. ?)
Schizopoda,	2	2		7 + 1	2	pr. (mes. ?)
Stomatopoda,	2	4		7 + 1	2	pr. (mes. ?)
Decapoda,	2	4		7 + 1	2	pr. (mes. ?)

A few features in the table require explanation. Among the number of cells recorded for the Estheridæ, the figure within the parenthesis under the head of Cone Cells indicates the occasional occurrence of cones containing only four cells, although the usual number is five. In the line for Serolis, under the head of Corneal Hypodermis, the parenthesis and included signs are intended to indicate the possibility of there being more than two cells in the corneal hypodermis for each ommatidium. In the Schizopods, Stomatopods, and Decapods, the number of proximal retinular cells is expressed in the form of 7 + 1 instead of 8, because one of the cells is rudimentary.

THE INNERVATION OF THE RETINA.

The innervation of the retina in the compound eyes of Crustaceans is chiefly interesting, because of its importance in relation to physiological questions. As this paper deals with a morphological topic, it would be obviously irrelevant to enter upon any extended discussion of this subject. Nevertheless, the innervation of the retina is not without some bearing on the general question which I have set for myself, and I shall therefore not pass it by, but put in as brief a form as possible what I have observed concerning it.

In my account of the retina in the lobster, I described the optic-nerve fibres as terminating in the proximal retinular cells. Near the ganglion each fibre consists of a bundle of fibrils, simply enclosed within a sheath, but as it approaches the retina it becomes coated with pigment. The pigment increases in quantity and the fibre correspondingly enlarges till it finally becomes continuous with the deeply pigmented retinular cell. The fibrillar axis can be distinguished in the pigmented portion of the fibre as a transparent axial structure, and it can also be traced distally through the pigment of each retinular cell till it breaks up into its ultimate fibrillæ, which are spread over the distal half of the rhabdome. This is the method of nerve termination in the lobster, and points very conclusively to the rhabdome as the terminal organ.

What I have seen of the termination of the nerve fibres in other Crustaceans confirms the account which I have already given for the lobster. In some species which I have studied, owing to the small size of the retinal elements, I was unable to determine the cells with which the nerve fibres connected. The termination of the fibres in the cells of the retinula was observed, however, in the following genera: Branchipus, Limnadia, Pontella, Gammarus, Talorchestia, Idotea, Porcellio, Sphæroma, Serolis, Gonodactylus, Mysis, Palæmonetes, Crangon, Cambarus, Palinurus, Pagurus, Cancer, and Cardisoma. In the majority of these, a fibrillar axis could be distinguished.[1] In Cambarus, as in Homarus, the nerve fibrillæ spread over the distal portion of the rhabdome.

In Serolis an exceptionally interesting condition is presented. At the level of the basement membrane each retinular cell contains a large fibrillar axis (Plate VI. Fig. 64, *ax. n.*). This becomes somewhat subdivided in the more distal portion of the cell, and in the region of the retinular nucleus it is represented by a cluster of several smaller axes (Fig. 63). At the level of the hyaline cell, these however cannot be distinguished (Fig. 62), but the scattered condition of the pigment granules in this plane is probably to be accounted for by the presence of many separate fibrils in the substance of the cell. In the region of the rhabdome an immense number of fine lines can be seen extending from the retinular cell into the substance of each rhabdomere (Fig. 61). These, I believe, represent the fibrils of the nervous axis. They have been previously observed in Serolis by Watase ('90, p. 291), and are so readily visible that there can be no question as to their presence. Each fibril is perpendicular to the longitudinal axis of the ommatidium, and extends through the rhabdomere to its axial surface. Before reaching this, however, the fibril passes through what seems to be a delicate membrane. When closely examined, this membrane often has the appearance of a row of dots instead of a line, and in several cases I have been unable to discover any traces of it. What its significance is, I am at a loss to say. As I have previously observed, when the elements of the retinula are separated the rhabdomere shows no tendency to break along this line. Since the structure is pierced by the fibrils, and does not appear to be a natural plane of rupture, and since sometimes it is apparently absent, I believe it may be considered, from a morphological standpoint at least, as a secondary and rather unimportant modification within the rhabdomere itself.

If I am correct in maintaining that the nerve fibrils in Serolis terminate in the rhabdomere, it is probable that they have a similar method of ending in all other Crustaceans, and in such instances as Homarus, where they have been traced only to the surface of the rhabdome, their actual termination has probably not been seen.

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[1] A definite fibrillar axis was traced from below the basement membrane to the region of the rhabdome in Gammarus (Plate I. Figs. 6–8), Porcellio (Plate V. Fig. 46), Idotea (Plate V. Figs. 53 and 55–57), Mysis (Plate VII. Figs. 87–89), Gonodactylus (Plate VIII. Figs. 101, 102), Palæmonetes (Plate IX. Figs. 116, 117), Cambarus, Pagurus, Cancer (Plate X. Figs. 130 and 131), and Cardisoma.

The termination of the fibrillæ of the optic nerve in the rhabdome supports Müller's belief that the nerve fibres terminate in a region near the proximal ends of the cones, and Grenacher's more specific view that they are connected with the retinular cells, and that the rhabdome is the terminal organ. This method of termination is not consistent with the opinion of Gottsche and Leydig, that the cone is the terminal organ, nor with Patten's rather similar belief that the ultimate nerve fibrillæ are distributed to the cone. I am therefore compelled to think that these authors are mistaken in their conclusion.

Theoretic Conclusions.

In attempting to account for the variation in the number of cells in different types of ommatidia, two courses naturally suggest themselves. Either the different kinds of ommatidia vary in the number of cells which they contain,. because they have had separate origins, or they are different because in some or all of them the ancestral ommatidium has suffered modification. An examination of the table on page 115 shows conclusively, I think, that in Crustaceans even the most extreme types are so little removed from one another that it is much more probable that the different kinds of ommatidia are genetically connected, than that they have been produced independently. Granting this statement, the question naturally arises, What are the means by which the primitive ommatidium was modified? I believe that a close scrutiny of the cellular structure of the ommatidia in living Crustaceans will disclose some of the factors in this process. There are at least three of these to be distinguished: the differentiation of cells, the suppression of cells, and the increase in the number of cells by cell division.

By the differentiation of cells, I do not mean the process by which hypodermal cells have become converted into retinular or cone cells, but that by which an element already differentiated in the ommatidium is secondarily modified to subserve another function. The only instance of this kind with which I am acquainted occurs among the retinular cells. In the majority of the simpler Crustaceans, the sides of the cones are covered with pigment, which is almost always contained in the distal ends of the retinular cells. In Serolis, among the Isopods, and apparently in all the genera of Stomatopods, Schizopods, and Decapods, the cones are surrounded by special pigment cells. These are always twice as numerous as the ommatidia, and represent, I believe, retinular cells which have become differentiated for the special purpose of sheathing the cones. The way in which this differentiation may have occurred has already been suggested in my paper on the lobster ('90ᵃ, p. 57).

Although I have expressed the opinion that these cells are to be regarded as modified retinular cells, it might be maintained that they are merely enlarged accessory pigment cells, such as occur in the interommatidial space of many Crustaceans. But I believe such an interpretation of these cells would be erroneous, for the following reason. In Serolis the nuclei of the pigment cells which surround the cone (Plate VI. Fig. 65, *nl. dst.*) possess one, and sometimes two, well marked nucleoli, but no fine chromatine granules. In this respect they closely resemble the nuclei of the proximal retinular cells (*nl. px.*), and differ considerably from those of the accessory pigment cells (*nl. h'drm.*). The nuclei of the last named cells contain only fine granules. So far, then, as their nuclei are concerned, the distal retinular cells bear a much closer resemblance to the proximal cells than to the accessory pigment cells. Each retinula in Serolis contains, moreover, only four cells, and in this respect differs considerably from other Isopods, where the number of retinular cells is either six or seven. On the supposition that the pigment cells surrounding the cone in Serolis are accessory pigment cells, one would be called upon to account for the exceptionally small number of cells in the retinula of this genus; whereas, if the cells around the cone are regarded as modified retinular cells, they may be taken to indicate for Serolis a primitive retinula composed of six cells, a number characteristic of the retinulæ in other Isopods. This interpretation of the condition of the retinula in Serolis is borne out by what is known of the retinula in Sphæroma, where, it will be remembered, a transition between the condition in Serolis and that in other Isopods was distinctly indicated.

In the Stomatopods, Schizopods, and Decapods, if my observations are correct, there are no ectodermic accessory pigment cells. Consequently, a comparison between these cells and what I have called the distal retinular cells cannot be drawn. In Mysis (Plate VII. Fig. 73), Gonodactylus (Plate VIII. Fig. 94), and Palæmonetes (Plate IX. Fig. 103), as well as in all other Decapods which I have examined, the resemblance between the nuclei of the retinular cells and those of the pigment cells which surround the cone is as striking as in Serolis, and suggests the origin of these cells from retinular cells rather than from any other source. In Homarus, the pigment cells around the cone present a condition of some interest in this connection. Each pigment cell is extended proximally as a long fibre, which certainly reaches nearly to the basement membrane, and probably passes through it in company with the fibrous ends of the retinular cells (compare Parker, '90^a, pp. 17–19). Admitting that these cells are merely modified accessory pigment cells, such a condition as this is quite unintelligible to me; but granting them to be differentiated retinular cells, their fibrous extensions can be easily explained as the rudiments of the fibrous portion of the cell with which the nerve fibre was once connected. A somewhat similar case occurs in Mysis, where the centre of each of the pigment cells which surround the cone contains a small transparent axis. This axis in every respect except that of connection with a nerve fibre corresponds to the fibrillar axes described in the functional retinular cells of this Crustacean (compare Plate VII. Figs. 77, 78, and 87). Consequently, the axis in the distal cells either represents a rudimentary nervous axis, in which case the cell containing it must be regarded as a retinular cell, or it is something for which I can suggest no explanation.

These facts lead me to conclude that the pigment cells which surround the cone in Serolis, the Stomatopods, Schizopods, and Decapods, are to be regarded as modified retinular cells, and I have therefore described them under the name of distal retinular cells, in contrast to proximal retinular cells, or those which retain their primitive position around the rhabdome. In the differentiation of a group of simple retinular cells into proximal and distal cells, the latter necessarily change their function from that of terminal nervous organs to that of screens chiefly concerned in excluding the light from the sides of the cones. Wherever the distal retinular cells occur, they afford evidence, I believe, that the structure of the ommatidium has undergone a modification from the primitive ommatidial condition.

The second method by which the structure of ommatidia may be changed, namely, the suppression of cells, is perhaps the one whose presence is most easily detected because of the frequent persistence of the partially reduced cells. These rudimentary cells can be identified most readily in the cases where they belong to groups in which the number of elements is constant for different ommatidia. I know of no evidence of suppression among the groups of cells in the corneal hypodermis or the cones. Among the retinulæ, however, it seems to be of rather common occurrence. The first indication of this process is naturally a diminution in the size of the cell to be suppressed. Such a step is perhaps shown in the retinula of Gammarus (Plate I. Fig. 6), where one of the five cells, although evidently functional, is nevertheless considerably reduced. Without much doubt, the body described in the retinula of Idotea robusta represents, for reasons already stated, the seventh cell present as a functional structure in Porcellio. In Idotea irrorata the retinulæ, with very few exceptions (Plate V. Fig. 54), contain only six cells, showing no trace of the seventh cell. This condition, I believe, is to be interpreted as one in which a cell has been completely suppressed. In Stomatopods, Schizopods, and Decapods the retinulæ have been shown to contain, in addition to the nuclei of the seven functional cells, an eighth nucleus, which may represent a rudimentary cell.

In all of the cases thus far cited, it might be maintained that what I have considered rudimentary cells are really cells newly acquired by the ommatidia, and not old cells gradually undergoing suppression. The condition in Idotea, however, where the body in question apparently contains no nucleus, would be difficult to explain on this assumption, whereas, if it be considered a cell undergoing reduction, its condition can be easily accounted for. In Stomatopods, Schizopods, and Decapods, the constancy in the number of cells and in the position of the eighth nucleus, the small amount of protoplasm which surrounds it, and the striking resemblance which it has to the other retinular nuclei, are facts difficult to explain on the assumption that it represents a newly acquired cell, but easily accounted for on the supposition that it is the remnant of a partially suppressed cell. For these reasons, I believe that the instances cited are valid cases of partial suppression, and that this must be regarded as one of the actual means employed in the modification of ommatidia.

That ommatidia have been modified by an increase in the number of their cells by cell division, is a proposition not easily established. The difficulty of obtaining conclusive evidence on this point can be made clear by an example. Let it be assumed that cones composed of two cells are converted by the division of the cells into cones composed of four cells. This step, even when first taken, would probably be accomplished during the embryonic growth of an animal, and therefore before the cones themselves had begun to be differentiated. What would actually happen would probably be this: the two cells, the homologues of which in all previous animals had given rise to two cone cells, would in this case each divide, thus producing a group of four cells, which ultimately would form a cone of four segments. If we could compare the adult animal in which such a process had occurred for the first time with its immediate ancestors, the only important difference that would be observed would be in the number of the cells in each cone, and if the genetic relations of the two individuals were not known, it could not be stated with certainty whether in one case we were dealing with an animal which had lost two cone cells or in the other, with one which had gained two; in other words, it would be impossible to determine which of the two conditions was the primitive one. The importance of embryological evidence in determining this question must therefore be apparent. But evidence from even this source might not be conclusive. Thus in the development of the lobster I have traced in detail the steps by which the ommatidia are formed, and although in this Crustacean the considerable number of cells in each ommatidium would warrant one in expecting some evidence of increase by division, the division of the cells in the retina is entirely accomplished some time before these elements show any grouping into ommatidia. Hence, the exact method of origin of the cells of the ommatidium cannot at present be given. I have observed that the same is also true in Gammarus; cell division is completed before the cells are grouped into ommatidia. Perhaps in the development of some other Crustaceans evidence of the kind which I have sought may be obtained, but in the few species which thus far have been studied the evidence has not been produced.

Although the supposition that ommatidia may increase the number of their cells by the division of those which they already possess is not supported by any direct observations with which I am acquainted, there are some facts recorded which are indirectly confirmatory of it. Thus, in Phyllopods, an increase in the number of cone cells appears to accompany a progressive differentiation of the retina itself. In this group, as I have already pointed out, the simplest condition of the retina is found in Branchipus and Apus. From the retina of Apus that of the Estheridæ can be easily derived, and the retina in the Estheridæ represents a condition from which the retina of the Cladocera may have arisen. That this series of retinas, from Apus through the Estheridæ to the Cladocera, is a natural one is abundantly proved by the course taken in the development of the eye in these groups. If we regard the condition of the cones in these Crustaceans, we shall find that in the most primitive retina, that of either Branchipus or Apus, they consist of four cells; that in the more complex retina of the Estheridæ they are usually composed of five cells, although cones of four cells are not unfrequent occurrences; and finally, that in the Cladocera they are always composed of five cells. Apparently in this series the development of the retina is paralleled by a corresponding development in the cones, whereby one composed of four cells is ultimately converted into one with five cells. Since the resemblance between any two of the cells in a cone composed of five elements is quite as close as that between the cells in cones containing only four elements, I believe that the additional cell, which has increased the number of segments from four to five, has been derived by the division of one of the original four cone cells, and not from an extra-ommatidial source.

Another instance of this kind occurs among the Isopods. The cones in this group, it will be remembered, are usually each composed of two segments. According to Beddard's figures ('90, Plate XXXI. Figs. 1 and 4) in Arcturus, however, they occasionally consist of three segments, and in Asellus aquaticus, according to Sars ('67, p. 110), although three of the four cones in each eye are composed of only two segments each, the fourth regularly contains three. The size of the segments in the fourth cone differs; two are small, and together their bulk about equals that of the third, and the last is approximately of the size of a segment in one of the other cones. If we attempt to explain the condition of the cone composed of three segments by supposing it to have been produced by adding to the normal pair of cone cells a single cell from some source external to the ommatidium, we are met with the difficulty, that what is apparently the added cell — the larger one — resembles more closely a segment in the other cones than do either of the two remaining cells, although the latter must on this assumption represent the original segments. If, however, we imagine the small segments to have arisen by the division of a single larger one similar to the large one which remains in the cone, the relation of the resulting segments both in size and number is a perfectly natural one. This explanation, therefore, seems to me to be more probable than the former. For these reasons, I believe that an increase in the number of cells in an ommatidium takes place by the division of the cells already forming a part of that ommatidium, rather than by the importation of new elements hitherto foreign to the ommatidium.

The conclusion which I would draw from the preceding discussion is, that there are at least three means of modifying the numerical formulæ of ommatidia, all of which involve only the cells primitively belonging to the ommatidium, and therefore do not necessitate the introduction of new cells from extra-ommatidial sources. They are cell differentiation, cell suppression, and cell multiplication.

Having now determined the means by which the cellular structure of the ommatidia in living Crustaceans is modified, we are prepared to approach the question of the structure of the primitive ommatidium. If it could be shown that ommatidia were modified only by increasing the number of their elements, it would naturally follow that those composed of the fewest cells would more nearly resemble the ancestral type than those which consist of many cells. On the other hand, if the suppression of cells were the only means employed in modifying structure, the ommatidia containing the greatest number of elements would most nearly approach the primitive type. Since, as I believe, both means are employed in the Crustacea, the determination of the structure of the ancestral ommatidium is evidently a difficult problem. Perhaps the most satisfactory way of attempting its solution is to consider separately the different categories of cells which enter into the formation of an ommatidium, and, after reviewing the conditions presented by each in different Crustaceans, to determine, if possible, which of these conditions is the most primitive. The conclusions thus arrived at concerning each kind of cell will afford the necessary grounds for the construction of an hypothetical formula of the ancestral ommatidium. Although it is not necessary that this ommatidium should be represented in any living Crustacean, for the ommatidia in all these may have suffered modification, yet it is possible that a representative of it may still exist.

Turning now to the consideration of the different groups of cells, we find that the corneal hypodermis presents two conditions; one in which its cells are not regularly arranged, and another in which they are grouped in pairs, each pair lying at the distal end of an ommatidium. The latter condition is characteristic of the Decapods, Schizopods, Stomatopods, Nebaliæ, Isopods, and some Branchiopods; the former, so far as is known, occurs in the Amphipods, the Branchiura, and in some Branchiopods (Limnadia and some species of Branchipus). In view of the fact that the corneal hypodermis is a part of the retina which retains the function of the general hypodermis but slightly modified, and that in the latter the cells do not present a regular arrangement, it is probable that a corneal hypodermis in which the cells are not regularly arranged is of a more primitive character than one in which they are definitely grouped.

The number of cells in the individual cones of Crustaceans varies from two to five. Cones composed of two cells occur in Eucopepoda, Amphipods, Isopods, and Schizopods; cones of three cells are present only exceptionally in Isopods; cones of four cells are found in the Decapods, Stomatopods, Nebaliæ, Branchiura, and some Branchiopods; cones of five cells characterize the Cladocera and some Branchiopods. I have already given reasons for regarding the cones composed of three cells as having been derived from those containing two, and cones composed of five cells from those possessing four. Since there is no evidence of degenerate cells in any of the cones composed of two segments, I am convinced that cones with four cells are derived from those with two cells, and not the reverse. On these grounds, I conclude that the most primitive form of cone in living Crustacea is that consisting of two cells.

The retinular cells in Crustaceans are subject to considerable variation. As I have previously shown, an ommatidium may contain one or two kinds. When there is only one kind, all the cells are grouped around the rhabdome, and are known simply as retinular cells. When there are two kinds, one occupies a position around the rhabdome, and the other around the cone; the former I have called proximal retinular cells, the latter distal retinular cells. Proximal and distal retinular cells occur in Serolis, the Stomatopods, Schizopods, and Decapods; simple retinular cells apparently characterize the ommatidia of all other Crustaceans. I have already presented reasons for considering the distal retinular cells as modified simple retinular cells, which, in the separation of the cone from the rhabdome by the elongation of the ommatidium, have lost their connection with the nervous element, but have retained their place next the dioptric one. A group of retinular cells in which this differentiation has occurred is not so primitive in its structure, therefore, as one in which all the retinular cells retain their original position around the rhabdome, as in the groups of Crustacea which possess simple retinular cells.

The number of simple retinular cells in Crustacean ommatidia varies from five to seven. In Nebalia, and some Isopods, the retinula contains seven cells; in other Isopods it is composed of six cells, and in the Branchiopods, the Cladocera, some Copepods, and Amphipods it consists of five cells. It is difficult to state which of these numbers represents the primitive condition. In the Isopods, as I have previously indicated (pp. 86 and 87), there is considerable evidence to show that a retinula composed of six cells has been produced from one containing seven by the suppression of one cell. Possibly in this way the retinula with five cells was derived from that with six, but I know of no observations which favor this supposition.

A small amount of indirect evidence on this question is to be obtained from the other structural peculiarities of the ommatidia containing retinulæ with five, six, or seven cells. These retinulæ occur in connection with two kinds of rhabdomes, — one in which the rhabdomeric segments are easily distinguishable, and the other from which they are apparently absent. Of these two kinds, the one in which the segments persist is evidently more primitive than the one in which their outlines are obliterated.

Probably in Nebalia, in which the retinula is composed of seven cells, and certainly in Idotea, where it consists of six, the rhabdome shows no indication of being composed of rhabdomeres, but in Porcellio the seven retinular cells surround a rhabdome composed of a corresponding number of rhabdomeric segments. In Branchipus, the retinula consists of five cells, but the rhabdome is apparently not composed of separable rhabdomeres, whereas in Pontella, Argulus, Gammarus, Talorchestia, Hyperia, and Phronima the five retinular cells are each represented by a rhabdomere. The more frequent occurrence of a primitive condition of rhabdome with the retinula having five cells than with that having seven, favors indirectly the idea that the retinula with the smaller number of cells is the more primitive of the two. The types of cones associated with the two kinds of retinulæ offer almost no evidence on the question in hand. Thus, a retinula of seven cells is associated with a cone of four cells in Nebalia, and with one of two cells in Porcellio, and a retinula of five cells is combined with a cone of four cells in Branchipus and Argulus, and with one of two cells in Amphipods. The relation of the two kinds of retinulæ to the corneal hypodermis affords some slight evidence in support of the opinion that the retinula of five cells represents the more primitive type; for although the differentiated type of corneal hypodermis — the one in which the cells are regularly arranged — may occur with either type of retinula, the undifferentiated hypodermis — in which the cells are not regularly grouped — is known to be associated only with retinulæ containing five cells (some Branchiopods, Argulus, and Amphipods). The evidence drawn from these various sources is obviously very slight; but such as it is, it indicates that the retinula with five cells, rather than that with a greater number, represents the more primitive condition. This conclusion receives some additional support from the fact that the retinula composed of five cells characterizes the ommatidia in a number of not otherwise very closely related Crustaceans (Pontella, Argulus, the Branchiopods, and Amphipods), whereas the type possessing seven cells occurs only among certain Isopods and in the Nebaliæ. I believe, therefore, that all the evidence at present deducible from the condition of the simpler retinulæ indicates that the one which contains five cells is more primitive than that composed of six or seven cells.

In the present argument I have purposely omitted any mention of the condition of the retinula in the Corycæidæ, those Copepods in which the lateral eyes present a highly modified condition. I have done this because I believe that the lateral eyes in many Copepods are degenerate, and that therefore the evidence to be drawn from them cannot be as trustworthy as that from other sources. That the lateral eyes in Copepods are degenerate, is shown from the fact that in many members of the group the eyes are entirely absent, and that in those in which they do occur, their structure is subject to considerable variation. Thus in Pontella the retina contains, besides one group of five retinular cells, three isolated nervous cells, whereas in Sapphirina there is a group of three retinular cells, and at least one isolated nervous cell. In Pontella, Sapphirina, Corycæus, and Copilia each retina is provided with a single lens, but in Irenæus, according to Claus ('63, Taf. II. Fig. 1), there are two lenses in each eye. These variations, including the total disappearance of the organ in some members of the group, lead me to believe that the lateral eyes in the Copepods are degenerated, and therefore are organs in which the suppression of cells may have reduced them to even a simpler condition than that presented by the ancestral ommatidium.

The conclusion which I draw from the preceding argument is, that the type from which the ommatidia in all living Crustaceans are probably derived would exhibit the following structures: a corneal hypodermis in which the cells are not regularly arranged, and consequently an unfacetted corneal cuticula; a cone composed of two cells; a retinula composed of five retinular cells and having a rhabdome which consists of five rhabdomeres. The retina of the primitive eye, a simple thickening in the superficial ectoderm, would be composed of ommatidia of this type arranged upon the hexagonal plan. None of the Crustaceans with which I am acquainted possess an eye of exactly this structure. The one in which this condition is most nearly represented is perhaps Gammarus. In this animal all the requirements of the hypothetical eye are fulfilled, except that the form of the retina as a whole is somewhat disturbed by the separation of the corneal hypodermis from the layer of the cones and retinulæ by a corneo-conal membrane, and by the partially disguised condition of the basement membrane.

If my conclusions be correct concerning the structure of the primitive ommatidium and the means by which it has been modified, it follows that the principal types of ommatidia have been produced mainly by increasing the number of cells in the primitive type, and that, of the three means of modifying the structure of ommatidia, cell division has been the most influential.

Although the hypothetical ommatidium which has been described in the preceding paragraphs has been spoken of as ancestral, it is not to be supposed that the condition which it presents must be regarded as necessarily its simplest form. I feel tolerably confident, however, that the primitive ommatidium must have been at least as simple as I have assumed it to be. Possibly its retinula may have been composed of less than five cells, as is that seen in some Copepods; although, as I have previously remarked, the condition of the lateral eyes in these Crustaceans is probably influenced by degeneration, and therefore may not represent a primitive stage. What might be regarded, however, as a more primitive form of ommatidium than that which I have described, may be seen in the eye of the Chætopod Nais (Carrière, '85, pp. 28, 29). In this worm the eye lies in the hypodermis on the side of the head, and consists of a few relatively large transparent cells, the proximal faces of which are in part covered by pigment cells. It is probable that the transparent cells are merely dioptric in function, and that the pigment cells are nervous. The transparent cells may therefore be looked upon as the forerunners of cone cells, and the pigment cells at their bases as retinular cells not yet differentiated into a retinula. It is not difficult to imagine the origin of an ommatidium from a single one of the transparent cells and its accompanying pigment cells, and, by an increase in the number of such groups, the production of a retina like that of the compound eye of Arthropods.

This view of the origin of the ommatidia in Arthropods is irreconcilable with that recently advanced by Watase ('90), according to whom each ommatidium is to be regarded as a pit formed by an involution of the hypodermis. The supposed cavity of this pit occupies nearly the whole length of the axial portion of the ommatidium, and is filled by the secretions of the cells constituting its wall. The secretion in the deeper part of the pit forms the rhabdome; that which is produced nearer its mouth, the cone. During the formation of the pit, the hypodermal cells are believed to retain such mutual relations that their morphologically distal ends lie next its cavity; hence the secretions produced by these ends, the rhabdome and cone, are to be regarded as modifications of the chitinous cuticula of the outer surface of the body.

Ingenious as this theory is, I have not been able to convince myself of its tenability. It may be urged against the assumption that the retinular cells occupy a proximal position and the cone cells a distal one on the wall of a hypodermal pocket, that in Gammarus the retinular cells extend from the distal to the proximal face of the retina, and that in Homarus the cone cells have a corresponding extent; these conditions show that it is possible to interpret the cells in an ommatidium as elements in a thickened epithelium, all of which originally extended from one face of the layer to the other, and the grouping of which is not even now interfered with by any process of involution. But granting that the retinal cells are thus arranged, it must be admitted that the surface on which the rhabdomeres are produced corresponds to the *sides* of the cells rather than to their *distal ends*. This interpretation of the position of the rhabdome is not, so far as I am aware, contrary to any well established facts, and indeed it is rather more in accordance with the condition seen in the eyes of some Arthropods than that implied in Watase's theory. Thus, in the lateral eyes of scorpions the retinal cells are arranged as in an ordinary epithelium, and the lateral wall of each cell is in part occupied by a rhabdomere. In this instance, then, it must be admitted either that the rhabdomeres are produced on the *sides* of the retinal cells, or that each cell has independently rotated upon itself, so as to bring its morphologically distal end into a position corresponding to the side of an ordinary epithelial cell. But there is neither direct evidence to show that this rotation of single cells has occurred, nor, in this case, can there be any motive assumed which might have induced the rotation of single elements. I therefore believe that in the lateral eyes of scorpions the rhabdomes are on the sides of the retinal cells in the strictest morphological sense; and if they can occur in this position in the eyes of scorpions, I can see no reason why they might not occur in similar positions on the retinal cells of compound eyes. Hence it seems to me as reasonable to interpret the retina in compound eyes as a layer of modified epithelium unaffected by involutions, as it is to consider it a layer in which each ommatidium represents an infolding.

When, moreover, an attempt is made to show how a particular ommatidium has arisen by involution, some difficulties are encountered. Thus in Gammarus, in which the ommatidium is of a primitive type, each ommatidial pocket would involve seven cells, two of which, the cone cells, must be imagined as forming the neck of the involution, while the remaining five, the retinular cells, would constitute the deeper portion of the pocket. The mechanical difficulty which would accompany the formation of an involution involving so small a number of cells must be obvious, and offers, I believe, an obstacle to the successful operation of the process assumed in Watase's theory.

The one instance in which Watase has described an actual involution to form the eyes in Arthropods is the lateral eye of Limulus. These eyes consist of a cluster of hypodermal pits, over each of which there is a cuticular lens. Although there cannot be the least doubt that in this case each pit is a hypodermal involution, the belief that each one is homologous with an ommatidium is by no means so well founded. In structure the wall of the pit differs considerably from that of an ommatidium; it contains no cells which can be definitely denominated, either as cone cells or as cells of the corneal hypodermis, and it does contain a large ganglionic cell, which is only questionably homologous with any element in an ommatidium. In most respects in which these pits differ from ommatidia, they resemble simple eyes, and I therefore regard them as such, rather than as representatives of an early condition in the formation of an ommatidium.

When to the objections raised in the preceding paragraphs the statement is added, that in both Homarus and Gammarus — representatives of the extremes of organization — the ommatidia are developed without showing any trace of infolding, Watase's theory of the formation of ommatidia by means of involutions appears in a still less favorable light. I therefore regard ommatidia, not as the result of involutions, but as differentiated clusters of cells in a continuous unfolded epithelium.

I have not observed anything that would lead to the conclusion recently expressed by Patten ('90), that an ommatidium is a hair-bearing sense bud. I believe, on the contrary, that they have had a very different origin.

In conclusion, I may add, that if my idea of the origin of ommatidia be correct, it supports Grenacher's opinion, that compound eyes are not derived directly from aggregations of simple eyes, but from groups of optic organs which were even more primitive in their structure than simple eyes. Possibly such primitive organs were the antecedents of both the compound and simple eyes of Arthropods, as Grenacher suggests; but possibly the two kinds of eyes may have had totally different origins.

BIBLIOGRAPHY.

Beddard, F. E.

'84. Preliminary Notice of the Isopods collected during the Voyage of H. M. S. "Challenger." — Part I. Serolis. Proceed. Zoöl. Soc. London, 1884. pp. 330–341. 1884.

'84ª. Report on the Isopoda Collected by H. M. S. Challenger during the Years 1873–76. Part I. The Genus Serolis. Voyage of the Challenger, Zoology. Vol. XI. pp. 1–85, Pls. I.–X. 1884.

'87. Note on a new Type of Compound Eye. Ann. Mag. Nat. Hist., Ser. V., Vol. XX. pp. 233–236. Sept., 1887.

'88. On the Minute Structure of the Eye in certain Cymothoidæ. Trans. Roy. Soc. Edinburgh, Vol. XXXIII. Pt. II. pp. 443–452, Pl. XXX. 1888.

'90. On the Minute Structure of the Eye in some Shallow-Water and Deep-Sea Species of the Isopod Genus Arcturus. Proceed. Zoöl. Soc. London, 1890, Pt. III. pp. 365–375, Pl. XXXI. Oct., 1890.

Bellonci, G.

'78. Morfologia del Sistema Nervoso Centrale della Squilla mantis. Ann. Mus. Civ. Storia Nat. Genova, Vol. XII. pp. 518–545, Tav. IV.–X. 1878.

'81. Sistema nervoso, ed organi dei sensi dello Sphæroma serratum. Atti R. Accad. Lincei, Transunti, Ser. 3, Vol. V. pp. 228, 229. 1881.

'81ª. Sistema nervoso e organi dei sensi dello Sphæroma serratum. Atti R. Accad. Lincei, Memorie, Ser. 3, Vol. X. pp. 91–103, Tav. I.–III. 1881.

Blanc, H.

'83. Observations faites sur la Tanais Oerstedii Kröyer. Zool. Anzeiger, Jahrg. VI. No. 154, pp. 634–637. Nov., 1883.

Bobretsky, N.

'73. Development of Astacus and Palæmon. Kiew, 1873. (The substance of this paper, so far as it refers to the eye, is known to me only through the abstract in Balfour's Comparative Embryology, Vol. II. pp. 397, 398. London, 1881.)

'74. Zur Embryologie des Oniscus murarius. Zeitschr. f. wiss. Zool., Bd. XXIV. pp. 179–203, Taf. XXI., XXII. 1874.

Brongniart, A.

'20. Mémoire sur le Limnadia, nouveau genre de Crustacés. Mém. Mus. Hist. Nat., Paris, Tom. VI. pp. 83–92, Pl. 13. 1820.

Bullar, J. F.

'79. On the Development of the Parasitic Isopoda. Philos. Trans. Roy. Soc. London, Vol. 169, pp. 505–521, Pls. 45–47. 1879.

Burmester, J.

'83. Beiträge zur Anatomie und Histologie von Cuma Rathkii Kr. Inaugural-Dissertation, Kiel. Kellinghausen, H. F. A. Lütje. 44 pp., 2 Taf. 1883.

Burmeister, H.

'35. Ueber den Bau der Augen bei Branchiopus paludosus (Chirocephalus Bén, Prévost). Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1835, pp. 529–534, Taf. XIII. Figs. 1–4. 1835.

'35a. Nachschrift zu Burmeister's Bemerkungen über den Bau der Augen bei Branchipus (s. p. 529). Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1835, p. 613. 1835.

Carrière, J.

'84. On the Eyes of Some Invertebrata. Quart. Jour. Micr. Sci., Vol. XXIV., New Ser., pp. 673–681, Pl. XLV. 1884.

'85. Die Sehorgane der Thiere vergleichend-anatomisch dargestellt. München und Leipzig, R. Oldenbourg. 6 + 205 pp., 147 Abbildungen und 1 Tafel. 1885.

'85a. Einiges über die Sehapparate von Arthropoden. Biologisches Centralblatt, Bd. V. No. 19, pp. 589–597. 1 Dec., 1885.

'89. Bau und Entwicklung des Auges der zehnfüssigen Crustaceen und der Arachnoiden. Biologisches Centralblatt, Bd. IX. No. 8, pp. 225–234. June, 1889.

Cavolini, P.

'92. Abhandlung über die Erzeugung der Fische und der Krebse. Aus dem Italiänischen übersetzt von E. A. W. Zimmermann. Berlin, In der Vossischen Buchhandlung. 6 + 192 pp., 3 Taf. 1792.

Chatin, J.

'77–78. Recherches pour servir à l'histoire du batonnet optique chez les crustacés et les vers. Ann. Sci. Nat., Sér. 6, Zool., Tom. V. Art. No. 9, pp. 1–45, 1877; Tom. VII. Art. No. 1, pp. 1–36, Pls. 1–3, 1878.

Claparède, E.

'60. Zur Morphologie der zusammengesetzten Augen bei den Arthropoden. Zeitschr. f. wiss. Zool., Bd. X. pp. 191–214, Taf. XII.–XIV. 1860.

Claus, C.

'59. Ueber das Auge der Sapphirinen und Pontellen. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1859, pp. 269–274, Fig. 1–3, Taf. V. B. 1859.

'62. Ueber Evadne mediterranea n. sp. und polyphemoides Lkt. Würzburger Naturwissenschaftliche Zeitschrift. Bd. III. pp. 238–246, Taf. VI. Figs. 1–5. 1862.

'63. Die frei lebenden Copepoden mit besonderer Berücksichtigung der Fauna Deutschlands, der Nordsee und des Mittelmeeres. Leipzig, Wilhelm Engelmann. 10 + 230 pp., 37 Taf. 1863.

Claus, C. (*continued*).

'65. Ueber die Organisation der Cypridinen. Zeitschr. f. wiss. Zool., Bd. XV. pp. 143–154, Taf. X. 1865.

'66. Die Copepoden-Fauna von Nizza. Marburg & Leipzig, N. G. Elwert'sche Buchhandlung. 34 pp., 5 Taf. 1866.

'71. Untersuchungen über den Bau und die Verwandtschaft der Hyperiden. Göttingen Nachrichten, pp. 149–157. 1871.

'72. Ueber den Körperbau einer australischen Limnadia und über das Männchen derselben. Zeitschr. f. wiss. Zool., Bd. XXII. pp. 355–364, Taf. XXIX., XXX. 1872.

'75. Ueber die Entwickelung, Organisation und systematische Stellung der Arguliden. Zeitschr. f. wiss. Zool., Bd. XXV. pp. 217–284, Taf. XIV.–XVIII. 1875.

'76. Zur Kenntniss der Organisation und des feinern Baues der Daphniden und verwandter Cladoceren. Zeitschr. f. wiss. Zool., Bd. XXVII. pp. 362–402, Taf. XXV.–XXVIII. 1876.

'77. Zur Kenntniss des Baues und der Organisation der Polyphemiden. Denkschr. K. Akad. Wissensch. Wien, Math.-Naturwiss. Cl., Bd. XXXVII. pp. 137–160, Taf. I.–VII. 1877.

'79. Der Organismus der Phronimiden. Arbeit. Zool. Inst. Wien, Tom. II. Heft 1, pp. 59–146, Taf. I.–VIII. 1879.

'86. Untersuchungen über die Organisation und Entwickelung von Branchipus und Artemia nebst vergleichenden Bemerkungen über andere Phyllopoden. Arbeit. Zool. Inst. Wien, Tom. VI. Heft 3, pp. 267–370, Taf. I.–XII. 1886.

'86^a. Ueber die Entwicklung und den feinern Baue der Stilaugen von Branchipus. Anzeiger K. Akad. Wissensch. Wien, Math.-Naturwiss. Cl., Jahrg. XXIII. Nr. VIII. pp. 60–63. 1886.

'87 Die Platysceliden. Wien, Alfred Hölder. 77 pp., 26 Taf. 1887.

'88. Ueber den Organismus der Nebaliden und die systematische Stellung der Leptostraken. Arbeit. Zool. Inst. Wien, Tom. VIII. Heft 1, pp. 1–148, 15 Taf. 1888.

Dana, J. D.

'50. Eyes of Sapphirina, Corycæus, etc. Amer. Jour. Sci. and Arts, Ser. 2, Vol. IX. p. 133. May, 1850.

Della Valle, A.

'88. Sopra le glandole glutinifere e sopra gli occhi degli Ampeliscidi del Golfo di Napoli. Atti Soc. Nat. Modena, Memorie, Ser. 3, Vol. VII. pp. 91–96. 1888.

Dohrn, A.

'67. Die embryonale Entwicklung des Asellus aquaticus. Zeitschr. f. wiss. Zool., Bd. XVII. pp. 221–278, Taf. XIV., XV. 1867.

'70. Untersuchungen über Bau und Entwicklung der Arthropoden. 4. Entwicklung und Organisation von Praniza (Anceus) maxillaris. Zeitschr. f. wiss. Zool., Bd. XX. pp. 55–80, Taf. VI.–VIII. 1870.

Frey, H., und R. Leuckart.

'47. Lehrbuch der Anatomie der wirbellosen Thiere. Leipzig, Leopold Voss. pp. 8 + 626. 1847.

'47ª. Beiträge zur Kenntniss wirbelloser Thiere mit besonderer Berücksichtigung der Fauna des Norddeutschen Meeres. Braunschweig, F. Vieweg und Sohn. 170 pp., 2 Taf. 1847.

Gegenbaur, C.

'58. Mittheilungen über die Organisation von Phyllosoma und Sapphirina. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1858, pp. 43–81, Taf. IV., V. 1858.

'58ª. Zur Kenntniss der Krystallstäbchen im Krustenthierauge. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1858, pp. 82–84. 1858.

'78. Elements of Comparative Anatomy. Translated by F. J. Bell. London, Macmillan & Co. 26 + 645 pp. 1878.

Gerstaecker, A.

'66–79. Crustacea (Erste Hälfte). *In* Klassen und Ordnungen des Thier-Reichs. Von Dr. H. G. Bronn. Leipzig und Heidelberg, C. F. Winter'sche Verlagshandlung, Bd. V. Abth. I. pp. 1–1320, Taf. I.–XLIX. 1866–79.

'81–90. Crustacea (Zweite Hälfte). Ibid., Bd. V. Abth. II. pp. 1–800, Taf. I.–LXVIII. [Incomplete.] 1881–90.

Gottsche, C. M.

'52. Beitrag zur Anatomie und Physiologie des Auges der Krebse und Fliegen. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1852, pp. 483–492, Taf. XI. Figs. 3–5. 1852.

Grenacher, H.

'74. Zur Morphologie und Physiologie des facettirten Arthropodenauges. Göttingen Nachrichten, pp. 645–656. 1874.

'77. Untersuchungen über das Arthropoden-Auge. Beilageheft zu den Klinischen Monatsblättern für Augenheilkunde, Jahrg. XV. Mai-Heft, pp. 1–42 [Separate?] 1877.

'79. Untersuchungen über das Sehorgan der Arthropoden, inbesondere der Spinnen, Insecten und Crustaceen. Göttingen, Vandenhoeck & Ruprecht, 8 + 188 pp., 11 Taf. 1879.

Grobben, C.

'79. Die Entwickelungsgeschichte der Moina rectirostris. Arbeit. Zool. Inst. Wien, Tom. II. Heft 2, pp. 203–268, Taf. I.–VII. 1879.

'81. Die Entwicklungsgeschichte von Cetochilus septentrionalis Goodsir. Arbeit. Zool. Inst. Wien, Tom. III. Heft 3, pp. 243–282, Taf. I.–IV. 1881.

Grube, E.

'65. Ueber die Gattungen Estheria und Limnadia und einen neuen Apus. Arch. f. Naturg., Jahrg. XXXI. Bd. I. pp. 203–282. 1865.

Häckel, E.

'64. Beiträge zur Kenntniss der Corycæiden. Jenaische Zeitschr., Bd. I. pp. 61–112, Taf. I.–III. 1864.

Herrick, F. H.

'86. Notes on the Embryology of Alpheus and other Crustacea, and on the Development of the Compound Eye. Johns Hopkins Univ. Circulars, Vol. VI. No. 54, pp. 42–44. Dec., 1886.

'88. The Development of Alpheus. Johns Hopkins Univ. Circulars, Vol. VII. No. 63, pp. 36, 37. Feb., 1888.

'89. The Development of the Compound Eye of Alpheus. Zool. Anzeiger, Jahrg. XII. No. 303, pp. 164–169. 1889.

'90. The Development of the American Lobster, Homarus americanus. Johns Hopkins Univ. Circulars, Vol. IX. No. 80, pp. 67, 68. April, 1890.

Hesse, M. E.

'58. Mémoire sur les Pranizes et les Ancées. Ann. Sci. Nat., Sér. 4, Zool., Tom. IX. pp. 93–119. 1858.

Hickson, S. J.

'85. The Retina of Insects. Nature, Vol. XXXI. pp. 341, 342. 12 Feb., 1885.

Huxley, T. H.

'57. Lectures on General Natural History. Lecture X. Medical Times and Gazette, New Ser., Vol. XIV. pp. 353–355. 11 April, 1857.

Jurine, L.

'06. Mémoire sur l'Argule foliacé (Argulus foliaceus). Ann. Mus. Hist. Nat., Paris, Tom. VII. pp. 431–458, Pl. 26. 1806.

Kingsley, J. S.

'86. The Development of Crangon vulgaris. Second Paper. Bull. Essex Inst., Salem, Vol. XVIII. Nos. 7–9, pp. 99–154. July, 1886.

'86ᵃ. The Arthropod Eye. Amer. Naturalist, Vol. XX. pp. 862–867. Oct., 1886.

'86ᵇ. The Development of the Compound Eye of Crangon. Zool. Anzeiger, Jahrg. IX. No. 234, pp. 597–600. 11 Oct., 1886.

'87. The Development of the Compound Eye of Crangon. Jour. Morphology, Vol. I. No. 1, pp. 49–66, Pl. II. Sept., 1887.

'89. The Development of Crangon vulgaris. Third Paper. Bull. Essex Inst., Salem, Vol. XXI. Nos. 1–3, pp. 1–42, Pls. I.–III. Jan., 1889.

Klunzinger, C. B.

'64. Beiträge zur Kenntniss der Limnadiden. Zeitschr. f. wiss. Zool., Bd. XIV., pp. 139–164, Taf. XVII.–XIX. 1864.

Lankester, E. R., and A. G. Bourne.

'83. The minute Structure of the Lateral and Central Eyes of Scorpio and of Limulus. Quart. Jour. Micr. Sci., Vol. XXIII., New Ser., pp. 177–212, Pls. X.–XII. Jan., 1883.

Lebedinski, J.

'90. Einige Untersuchungen über die Entwicklungsgeschichte der Seekrabben. Biologisches Centralblatt, Bd. X. Nr. 5, 6, pp. 178–185. May, 1890.

Lemoine, V.

'68. Recherches pour servir à l'histoire des systèmes nerveux musculaire et glandulaire de l'écrevisse. Ann. Sci. Nat., Sér. 5, Zool., Tom. IX. pp. 99–280, Pls. 6–11. 1868.

Lenz, H.

'77. Estheria californica, Pack. Arch. f. Naturg., Jahrg. XLIII., Bd. I. pp. 24–40, Taf. III., IV. 1877.

Lereboullet, A.

'43. Mémoire sur la Ligidie de Persoon. Ann. Sci. Nat., Sér. 2, Zool., Tom. XX. pp. 103–142, Pls. 4, 5. 1843.

'53. Mémoire sur les Crustacés de la famille des Cloportides qui habitent les environs de Strasbourg. Mém. Soc. Mus. Hist. Nat., Strasbourg, Tom. IV. 2^e et 3^e Livraisons, pp. 1–130, Pls. I.–X. 1853.

Leuckart, R.

'59. Carcinologisches. Arch. f. Naturg., Jahrg. XXV., Bd. I. pp. 232–266, Taf. VI., VII. 1859.

'75. Organologie des Auges. *In* Handbuch der gesammten Augenheilkunde redigirt von Graefe und Saemische. Band II., Erste Hälfte, Zweiter Theil, Erste Hälfte, pp. 145–301. 1875.

Leydig, F.

'50. Ueber Argulus foliaceus. Zeitschr. f. wiss. Zool., Bd. II. pp. 323–349, Taf. XIX., XX. 1850.

'51. Ueber Artemia salina und Branchipus stagnalis. Zeitschr. f. wiss. Zool., Bd. III. pp. 280–307, Taf. VIII. 1851.

'55. Zum feineren Bau der Arthropoden. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1855, pp. 376–480, Taf. XV.–XVIII. 1855.

'57. Lehrbuch der Histologie des Menschen und der Thiere. Frankfurt a. M., Meidinger Sohn & Co. 12 + 551 pp. 1857.

'60. Naturgeschichte der Daphniden (Crustacea Cladocera). Tübingen, Laupp und Siebeck. 4 + 252 pp., 10 Taf. 1860.

'64. Tafeln zur Vergleichenden Anatomie. Tübingen, Laupp & Siebeck. Erstes Heft, 10 Tafeln nebst Erklärungen. 1864.

'64^a. Das Auge der Gliederthiere. Tübingen, Laupp & Siebeck. 50 pp. 1864.

'78. Ueber Amphipoden und Isopoden. Zeitschr. f. wiss. Zool., Bd XXX., Supplement, pp. 225–274, Taf. IX.–XII. May, 1878.

Lubbock, J.

'88. On the Senses, Instincts, and Intelligence of Animals, with Special Reference to Insects. New York, D. Appleton & Co. 29 + 292 pp. The International Scientific Series, Vol. LXIV. 1888.

Mayer, P.

'82. Die Caprelliden des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna und Flora des Golfes von Neapel, VI. Monographie, 10 + 201 pp., 10 Taf. 1882.

Milne Edwards, H.

'34. Histoire naturelle des Crustacés, comprenant l'Anatomie, la Physiologie et la Classification de ces Animaux. Tome Premier. Paris, Rovet. 35 + 468 pp. 1834.

Müller, F.

'64. Ueber den Bau der Scheerenasseln (Asellotes héréropodes M. Edw.). Arch. f. Naturg., Jahrg. XXX. Bd. I. pp. 1–6. 1864.

Müller, J.

'26. Zur vergleichenden Physiologie des Gesichtssinnes des Menschen und der Thiere, nebst einem Versuch über die Bewegungen der Augen und über den menschlichen Blick. Leipzig, C. Cnoblock. 32 + 462 pp., 8 Tab. 1826.

'29. Fortgesetzte anatomische Untersuchungen über den Bau der Augen bei den Insekten und Crustaceen. Arch. f. Anat. u. Physiol. (Meckel), Jahrg. 1829, pp. 38–64, Taf. III. Figs. 1–17. 1829.

'29ª. Sur les yeux et la vision des Insectes, des Arachnides et des Crustacés. Ann. Sci. Nat., Tom. XVII. pp. 225–253 and 365–386; Tom. XVIII. pp. 73–106. 1829.

'31. Ueber den Bau der Augen bei Argulus foliaceus mit Bemerkungen über die Eintheilung der Crustaceen nach dem Bau der Augen. Zeitschr. f. Physiol., Bd. IV. Heft 1, pp. 97–105, Taf. VI. Figs. 5, 6. 1831.

'35. Anmerkung des Herausgebers. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1835, pp. 613, 614. 1835.

'52. Anmerkung des Herausgebers. Arch. f. Anat., Physiol. u. wiss. Med., Jahrg. 1852, p. 492. 1852.

Newton, E. T.

'73. The Structure of the Eye of the Lobster. Quart. Jour. Micr. Sci., New Ser., Vol. XIII. pp. 325–343, Pls. XVI., XVII. 1873.

Nusbaum, J.

'87. L'embryologie de Mysis chameleo (Thompson). Arch. Zool. exp. et gén., Sér. 2, Tom. V. pp. 123–202, Pls. V.–XII. 1887.

Owen, R.

'43. Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals. London: Longman, Brown, Green, and Longmans. 392 pp. 1843.

Pagenstecher, H. A.

'61. Phronima sedentaria. Arch. f. Naturg., Jahrg. XXVII. Bd. I. pp. 15–41. 1861.

Parker, G. H.

'90. A Preliminary Account of the Development and Histology of the Eyes in the Lobster. Proc. Amer. Acad. Arts and Sci., Vol. XXIV. pp. 24, 25. 1890.

'90ª. The Histology and Development of the Eye in the Lobster. Bull. Mus. Comp. Zoöl., Vol. XX. No. 1, pp. 1–60, 4 Pls. May, 1890.

Parsons, G.

'31. An Account of the Discoveries of Müller and others in the Organs of Vision of Insects and the Crustacea. Magazine of Natural History, Edinburgh, Vol. IV. pp. 124–134, 220–234, and 363–372. 1831.

Patten, W.

'86. Eyes of Molluscs and Arthropods. Mittheilungen Zool Station zu Neapel, Bd. VI. Heft IV. pp. 542–756, Taf. 28–32. June, 1886.

'90. Is the Ommatidium a Hair-bearing Sense-Bud? Anat. Anzeiger, Jahrg. V. Nos. 13, 14, pp. 353–359. July, 1890.

Pereyaslawzewa, S.

'88. Le Développement de Gammarus poecilurus, Rthk. (Études sur le développement des Amphipodes, Première Partie.) Bull. Soc. Impér. Naturalistes de Moscou, Nouvelle Sér., Tom. II. No. 2, pp. 185–219, Pls. III.–VI. 1888.

Reichenbach, H.

'86. Studien zur Entwicklungsgeschichte des Flusskrebses. Abhandl. Senckenb. Naturf. Gesellsch., Bd. XIV. Heft 1, pp. 1–137, Taf. I.–XIV. 1886.

Rossiiskaya, M.

'89. Le Développement d'Orchestia littorea, Spence Bate. (Études sur le développement des Amphipodes, Deuxième Partie.) Bull. Soc. Impér. Naturalistes de Moscou, Nouvelle Sér., Tom. II. No. 4, pp. 561–581, Pls. XVI., XVII. 1889.

Rossiiskaya-Koschewnikowa, M.

'90. Développement de la Sunamphitoë valida, Czerniavski, et de l'Amphitoë picta, Rathke. (Études sur le développement des Amphipodes, Quatrième Partie.) Bull. Soc. Impér. Naturalistes de Moscou, Nouvelle Sér., Tom. IV. No. 1, pp. 82–103, Pls. I., II. 1890.

Sars, G. O.

'67. Histoire naturelle des Crustacés d'eau douce de Norvège. Les Malacostracés. Christiania, Chr. Johnsen. 155 pp., 10 Pls. 1867.

Schäffer, J. C.

'56. Der krebsartige Kiefenfuss mit der kurzen und langen Schwanzklappe. Regensburg, E. A. Weiss. 142 pp. 7 Taf., 1756.

Schmidt, O.

'78. Die Form der Krystallkegel im Arthropodenauge. Zeitschr. f. wiss. Zool., Bd. XXX., Supplement, pp. 1–12, Taf. I. 1878.

Schultze, M.

'67. Ueber die Endorgane des Sehnerven im Auge der Gliederthiere. Arch. f. mikr. Anat., Bd. III. pp. 404–408. 1867.

'68. Untersuchungen über die zusammengesetzten Augen der Krebse und Insecten. Bonn, Cohen & Sohn. 32 pp., 2 Taf. 1868.

Schultze, M. (*continued*).

'68^a. Bemerkungen zu dem Aufsatze des Dr. W. Steinlin. Arch. f. mikr. Anat., Bd. IV. pp. 22–25. 1868.

Spangenberg, F.

'75. Zur Kenntniss von Branchipus stagnalis. Zeitschr. f. wiss. Zool., Bd. XXV., Supplement, pp. 1–64, Taf. I.–III. 1875.

'76. Ueber Bau und Entwicklung der Daphniden. Göttingen Nachrichten, pp. 517–537. 1876.

Stebbing, T. R. R.

'88. Report on the Amphipoda collected by H. M. S. Challenger during the Years 1873–1876. The Voyage of H. M. S. Challenger, Zoölogy, Vol. XXIX. 1888.

Steinlin, W.

'66. Beiträge zur Anatomie der Retina. Bericht St. Gallischen naturwiss. Geselsch., 1865–66, pp. 17–138, Taf. I.–III. 1866.

'68. Ueber Zapfen und Stäbchen der Retina. Arch. f. mikr. Anat., Bd. IV. pp. 10–21, Taf. II. 1868.

Straus, H. E.

'19. Mémoire sur les Daphnia, de la classe des Crustacés, Première Partie. Mém. Mus. Hist. Nat., Tom. V. pp. 380–425, Pl. 29. 1819.

Swammerdam, J.

'52. Bibel der Natur. Edition Hermann Boerhave. Aus dem Holländischen übersetzt. Leipzig, J. F. Gleditschen. pp. 12 + 410 + Register, Tab. I.–LIII. 1752.

Sye, C. G.

'87. Beiträge zur Anatomie und Histologie von Jaera marina. Inaugural-Dissertation. Kiel, C. Böckel. 37 pp., 3 Taf. 1887.

Treviranus, G. R. und L. C.

'16. Vermischte Schriften anatomischen und physiologischen Inhalts. Erster Band. Göttingen, J. F. Röwer. 8 + 188 pp., 16 Taf. 1816.

Watase, S.

'89. On the Structure and Development of the Eyes of the Limulus. Johns Hopkins Univ. Circulars, Vol. VIII. No. 70, pp. 34–37. March, 1889.

'90. On the Morphology of the Compound Eyes of Arthropods. Studies Biol. Lab. Johns Hopkins Univ., Vol. IV. No. 6, pp. 287–334, Pls. XXIX.–XXXV. Feb, 1890.

'90^a. On the Migration of the Retinal Area, and its Relation to the Morphology of the Simple Ocelli and the Compound Eyes of Arthropods. Johns Hopkins Univ. Circulars, Vol. IX. No. 80, pp. 63–65. April, 1890.

'90^b. On the Morphology of the Compound Eyes of Arthropods. Quart. Jour. Micr. Sci., Vol. XXXI. Pt. II. pp. 143–157, Pl. XIX. June, 1890.

Weismann, A.

'74. Ueber Bau und Lebenserscheinungen von Leptodora hyalina Lilljeborg. Zeitschr. f. wiss. Zool., Bd. XXIV. pp. 349–418, Taf. XXXIII.–XXXVIII. 1874.

Will, F.

'40. Beiträge zur Anatomie der zusammengesetzten Augen mit facettirter Hornhaut. Leipzig, Leopold Voss. 32 pp., 1 Taf. 1840.

Zaddach, E. G.

'41. De Apodis cancriformis Schæff. Bonnæ, Typis Caroli Georgii. 72 pp., 4 Tab. MDCCCXXXXI.

Zenker, W.

'54. Monographie der Ostracoden. Arch. f. Naturg., Jahrg. XX. Bd. I. pp. 1–87, Taf. I.–VI. 1854.

EXPLANATION OF FIGURES.

All the drawings were made with the aid of an Abbé camera. Unless otherwise stated, the specimens from which the drawings were made were stained in Czokor's alum-cochineal and mounted in benzol-balsam. The reagent used in depigmenting sections was an aqueous solution of potassic hydrate $\frac{1}{4}\%$.

ABBREVIATIONS.

a.	Anterior.
ax. n.	Axis of nerve fibrillæ.
brs. oc.	Optic pocket.
cl. con.	Cone cell.
cl. crn.	Cell of corneal hypodermis.
cl. dst.	Distal retinular cell.
cl. hyl.	Hyaline cell.
cl. ms'drm.	Mesodermic cell.
cl. px.	Proximal retinular cell.
cl. rtn.'	Retinular cell.
cl. rud.	Rudimentary retinular cell.
cnch.	Shell.
cœl.	Body cavity.
con.	Cone.
cp. sng.	Blood corpuscle.
crn.	Corneal cuticula.
cta.	Cuticula.
d.	Dorsal.
dsc.	Sucking disk.
dx.	Right.
gn. opt.	Optic ganglion.
h'drm.	Hypodermis.
hp.	Liver.
in.	Intestine.
lns.	Lens.
mb. ba.	Basement membrane.
mb. crn.	Corneal membrane.
mb. crn'con.	Corneo-conal membrane.
mb. i'cl.	Intercellular membrane.
mb. n. opt.	Membrane of optic nerve.
mb. pi'ph.	Peripheral membrane.
mb. pr'con.	Preconal membrane.
mu.	Muscle.
n. fbr.	Nerve fibre.
nl. con.	Nucleus of cone cell.
nl. crn.	Nucleus of cell in corneal hypodermis.
nl. dst.	Nucleus of distal retinular cell.
nl. h'drm.	Nucleus of hypodermal cell.
nl. hyl.	Nucleus of hyaline cell.
nl. ms'drm.	Nucleus of mesodermic cell.
nl. px.	Nucleus of proximal retinular cell.
nl. rtn.'	Nucleus of retinular cell.
n. opt.	Optic nerve.
oc.	Eye.
omm.'	Ommateum.
p.	Posterior.
po. brs.	Pore of optic pocket.
r.	Retina.
rhb.	Rhabdome.
rhb'm.	Rhabdomere.
rtn.'	Retinula.
s.	Left.
v.	Ventral.
va. sng.	Blood-vessel.

Such other abbreviations as have been used are explained in the description of the figures with which they occur.

PLATE I.

Gammarus.

Fig. 1. A section of the right eye in a plane transverse to the chief axis of the body and through the central part of the retina. × 115.

" 2. A section lengthwise of an ommatidium. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and mark the levels at which the latter were taken. × 475.

" 3. A transverse section in the plane of the corneal hypodermis. × 475.

" 4. A transverse section through the distal ends of the retinular cells and cone. × 475.

" 5. A transverse section through the proximal portion of the cone and through the adjoining retinular cells. × 475.

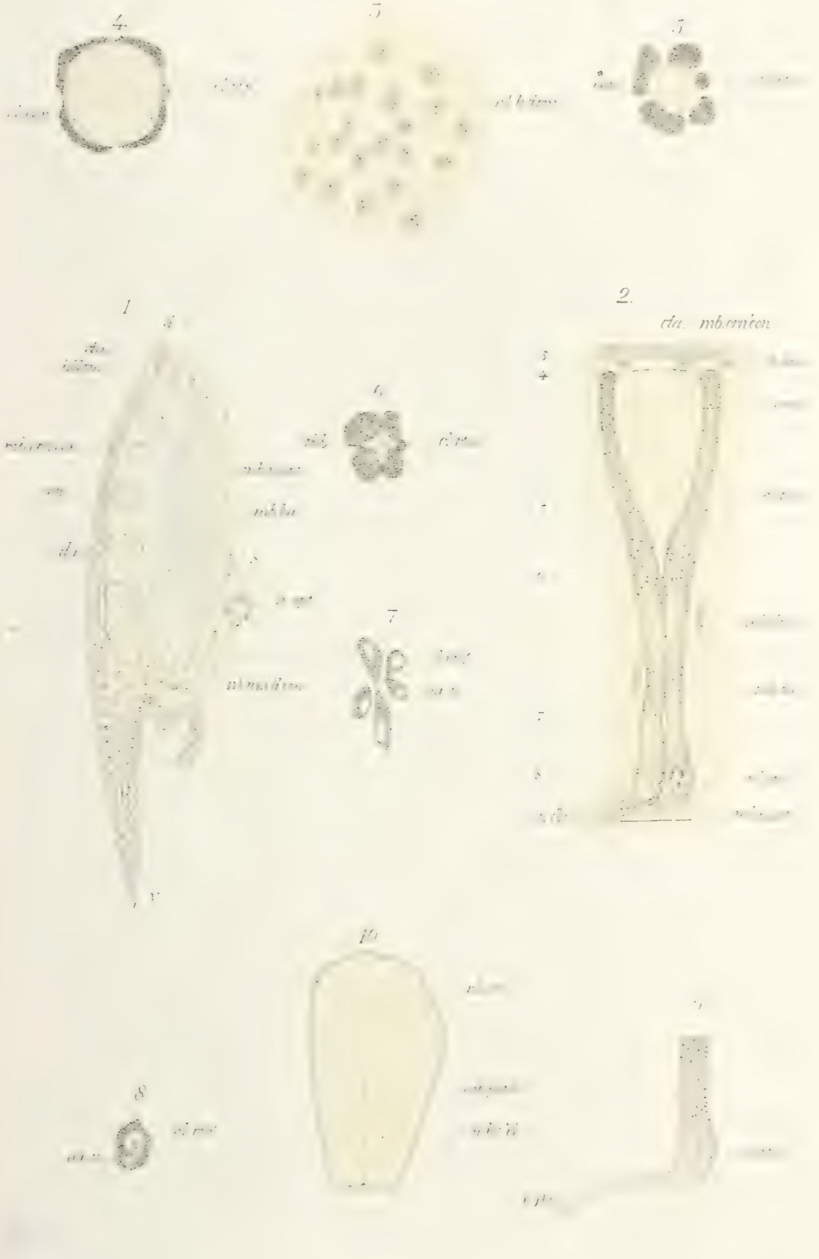
" 6. A transverse section through the retinula in the region of the rhabdome. × 475.

" 7. A transverse section through the retinular cells somewhat proximal to the basement membrane. × 475.

" 8. A transverse section through a single retinular cell in the region of its nucleus. × 475.

" 9. The proximal portion of a retinular cell viewed from the side. (Compare Fig. 2.) Isolated in Müller's fluid. Not stained. × 475.

" 10. A cone isolated in Müller's fluid and viewed from the side. Not stained. × 475.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GAMMARUS.

B. Meisel lith. Boston

PLATE II.

Argulus.

(Figs. 11–17.)

Fig. 11. A section in a plane transverse to the chief axis of the body and through the right eye. Depigmented. × 140.

" 12. A longitudinal section of an ommatidium. × 475.

" 13. A longitudinal section of an ommatidium which had been depigmented. The numbers at the left of the figure correspond to the numbers of the four following figures of transverse sections, and mark the levels at which the latter were made. × 475.

" 14. A transverse section through the distal end of a cone and the surrounding pigment cells. × 475.

" 15. A transverse section through the proximal portion of a group of four cone cells. The intercellular membranes of the cells present four thickened regions. × 475.

" 16. A transverse section through the rhabdome. Depigmented × 475.

" 17. A transverse section through the retinula somewhat proximal to the rhabdome. × 475.

Pontella.

Fig. 18. The left lateral eye seen from the left side. The section is an optical one; its plane is very nearly parallel to the sagittal plane of the body. Depigmented in alcohol (see p. 78). × 275.

" 19. A transverse section of the optic nerve from a region immediately posterior to the retina. The sagittal plane divides the nerve into symmetrical halves; the fibres in each half belong exclusively to the lateral eye of the corresponding side. × 400

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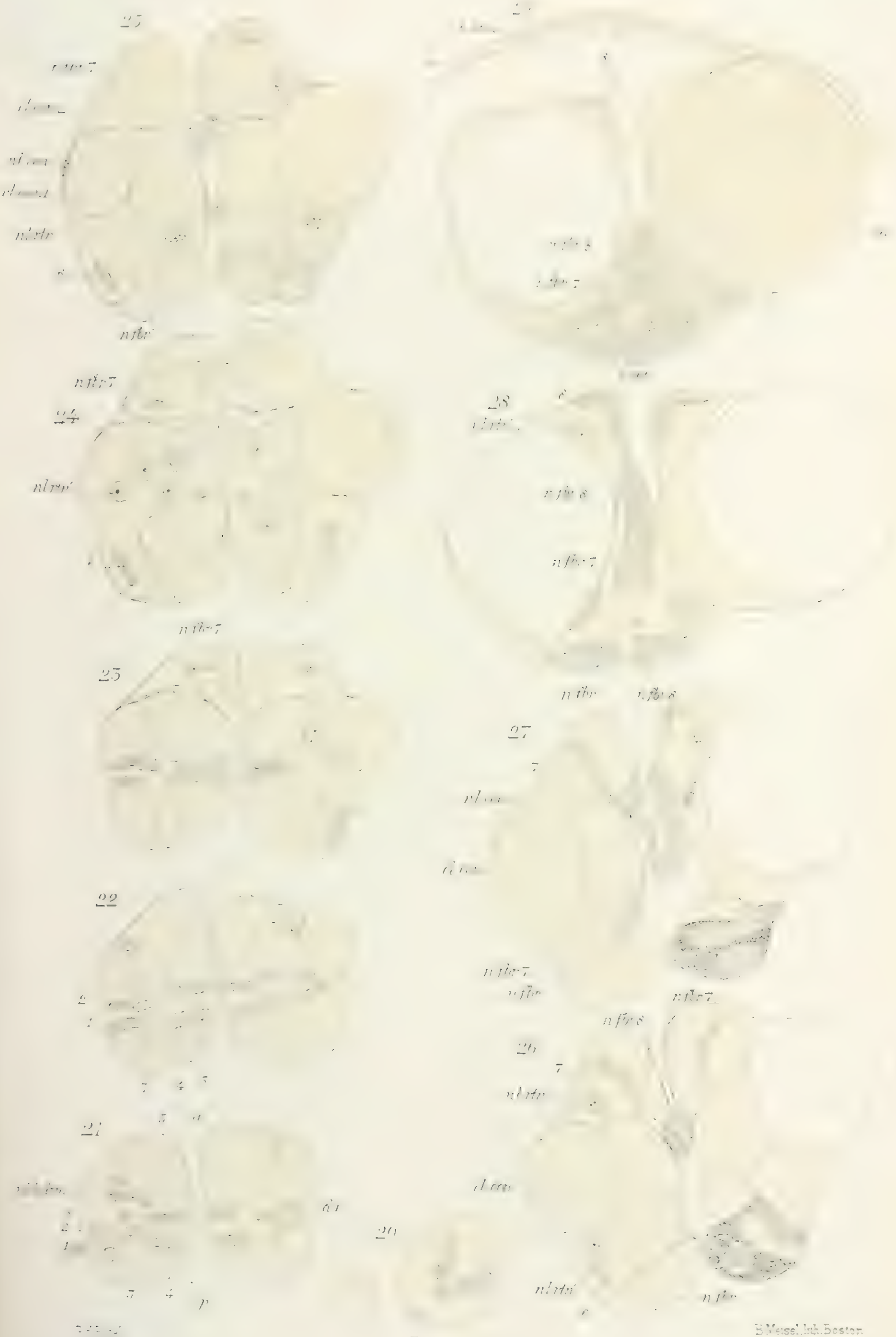
B. Meisel lith. Boston

COPEPODA.

PLATE III.

Pontella.

Figs. 20–29. A complete series of ten consecutive sections through the right and left retinas in planes parallel to the horizontal plane of the animal. The sections are viewed from their dorsal faces. Figure 20 represents the most ventral section; Figure 29, the most dorsal. The plane of Figure 25 is approximately indicated by the incomplete dotted line *mu. con.* in Figure 18 (Plate II.). In the sections on the present plate the different bodies in the left retina have been designated by appropriate letters and figures. The eight rhabdomeres have been indicated simply by numbers; the same number always refers to the same rhabdomere. For the sake of distinction, the two cone cells have been marked *cl. con. 1* and *cl. con. 2*. Some of the nerve fibres (*n. fbr. 7* and *n. fbr. 8*) have been numbered in reference to the particular rhabdomeres with which they are associated. × 400.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PONTELLA.

B. Meisel, lith. Boston.

PLATE IV.

Branchipus.

(Figs. 30–32.)

Fig. 30. A longitudinal section of an ommatidium. × 400

" 31. A transverse section through the distal end of four cones. × 400.

" 32. A transverse section through the middle portion of a retinula. × 400.

Limnadia.

(Figs. 33–39.)

Fig. 33. A section through the anterior part of the body, including the eye, in a plane transverse to the chief axis. × 25.

" 34. An enlarged portion of a section from the same series as that from which Figure 33 was drawn, but in a position slightly anterior to the latter. × 115.

" 35. A section through the eye cut in the sagittal plane of the animal. Depigmented. × 90.

" 36. A lateral view of an ommatidium. The numbers at the left of the figure correspond to the numbers of the three following figures of transverse sections, and mark the levels at which the latter were taken. × 475.

" 37. A transverse section through the corneal hypodermis and distal ends of the cones. × 475.

" 38. A transverse section through four cones at the level where they are thickest. × 475.

" 39. A transverse section through the central portion of four retinulæ. × 475.

Evadne.

(Figs. 40–45.)

Fig. 40. An optical section through the eye and adjoining structures in a plane approximately parallel to the sagittal plane of the body, but lying somewhat to the right of it. × 140.

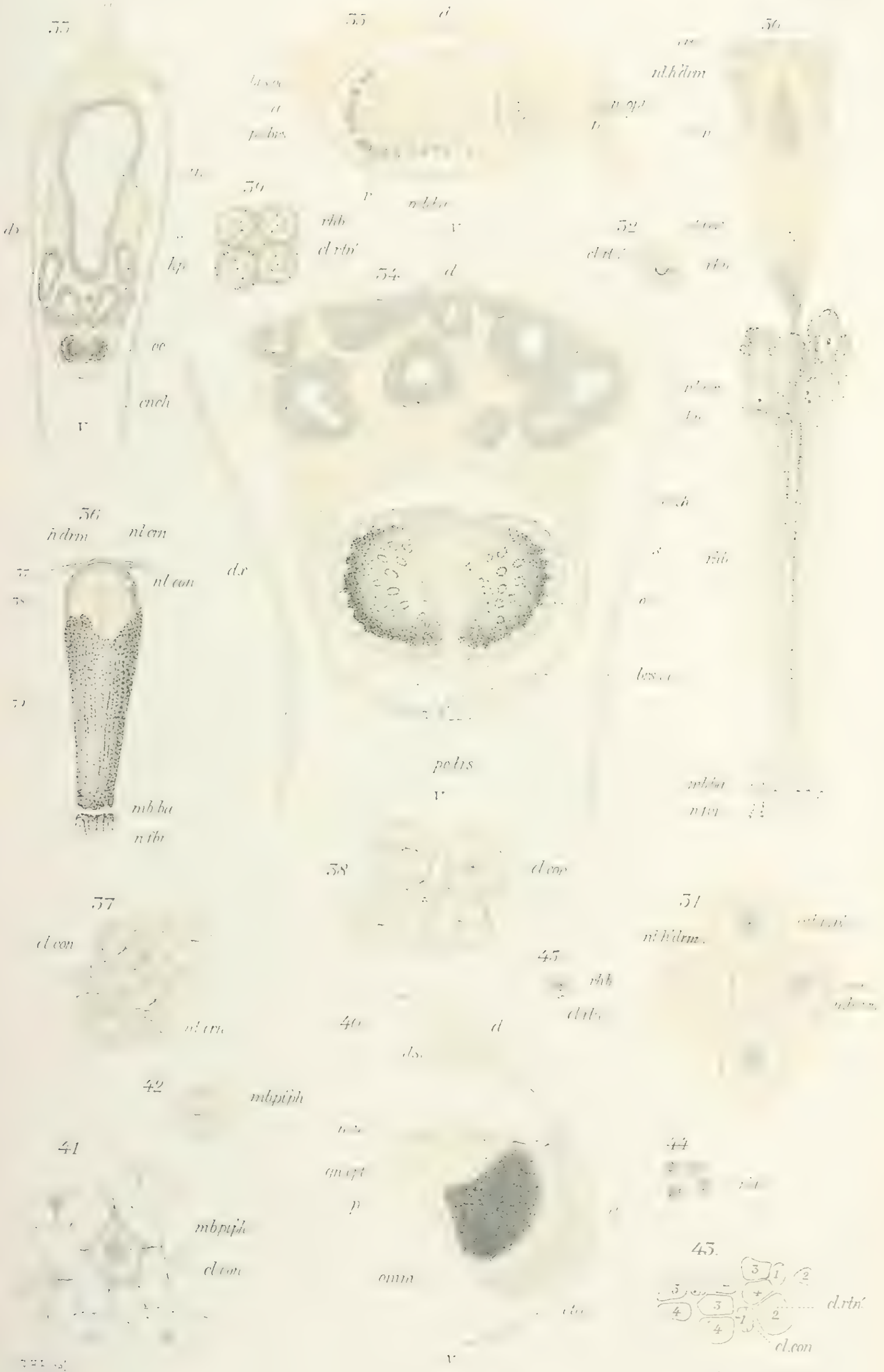
" 41. A transverse section through the distal ends of the cones. × 475.

" 42. A transverse section through the proximal end of a cone. × 475.

" 43. A transverse section through the distal ends of three groups of retinular cells. In each group the corresponding cells have been designated by the same number. × 475.

" 44. A transverse section through the central part of four rhabdomes. × 475.

" 45. A transverse section through a retinula. Depigmented. Kleinenberg's alum-hæmatoxylin. × 475.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PHYLLOPODA.

G.H.P. del.
B Meisel lith. Boston.

PLATE V.

Porcellio.

Fig. 46. A transverse section through a retinula in a plane slightly distal to the basement membrane. The single, light, central spot represents the proximal end of the rhabdome. × 475.

Idotea robusta, Kroyer.

(Figs. 47, 48.)

Fig. 47. A transverse section through the distal end of a retinula. The bodies, one of which is marked x, are spheres of coagulated material which occur in the interommatidial spaces, and which have been brought into prominence by the action of the hardening reagent. × 475.

" 48. A transverse section through three ommatidia in the region of their rhabdomes. × 475.

Idotea irrorata, M. Edws.

(Figs. 49–57.)

Fig. 49. The anterior face of a section transverse to the chief axis of the body, and passing through the eye on the right side of the head. × 140.

" 50. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of the following six figures of transverse sections and mark the levels at which the latter were taken. × 475.

" 51. A transverse section through the distal ends of the cones. × 475.

" 52. A transverse section through the middle region of a cone. × 475.

" 53 A transverse section through the middle of a retinula. Near the centre of each cell can be seen a small axis of nerve fibrillæ. × 475.

" 54. A transverse section through a retinula composed of seven cells instead of six. This section was cut approximately at the same level as that shown in the preceding figure. × 475.

" 55. A transverse section through a retinula near its proximal end. Each fibrillar axis is much larger at this plane than in that shown in Figure 53 × 475.

" 56. A transverse section of several groups of retinular cells immediately proximal to the basement membrane. × 475.

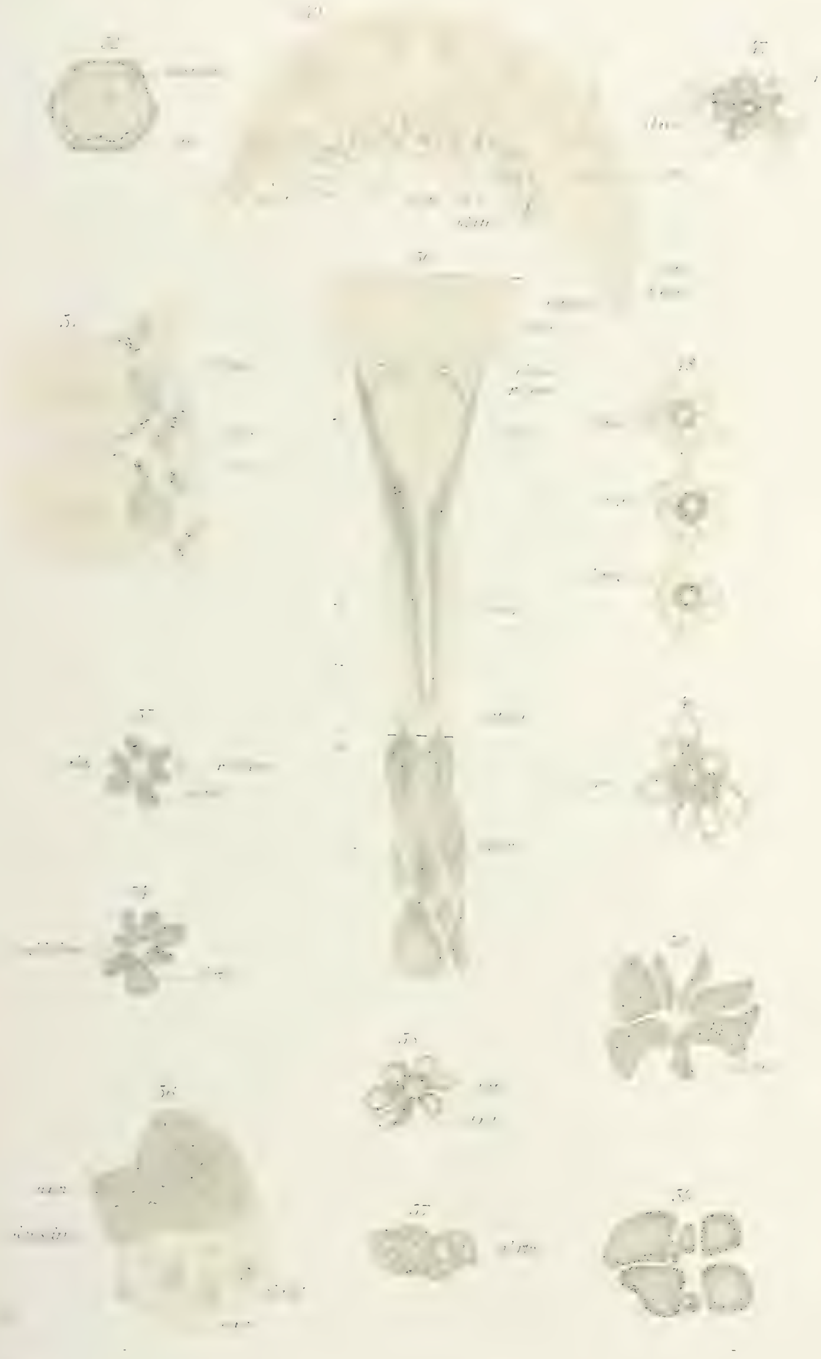
" 57. A transverse section of four retinular cells at the level in which their nuclei occur. The axis of nerve fibrillæ in the plane of this section and in that of the preceding one (Fig. 56) are smaller than they are at the base of the retina (compare Fig. 55).

Sphæroma.

(Figs. 58, 59.)

Fig. 58. A transverse section of a retinula at a level slightly distal to the basement membrane. × 475.

" 59. A transverse section of the fibrous ends of the cells from a single retinula. The plane of section is slightly proximal to the basement membrane. The only indication of an axis of nerve fibrillæ is the more transparent condition of the central part of the cells, due to the partial absence of pigment granules. × 475.



ISOPODA.

B. Meisel lith. Boston.

PLATE VI.

Serolis.

Figures 60 to 64 inclusive represent the structure of the ommatidium in the adult. Figures 65 to 72 are drawn from sections of ommatidia in well advanced embryos. All figures are magnified 475 diameters.

Fig. 60. A tangential section through the most distal portion of the retina. This section includes a portion of a cone and the tissue lying between it and two adjoining cones.

" 61. A transverse section of a retinula in the region of its rhabdome. The arrangement of the pigment granules and nerve fibrillæ is indicated in only one of the four cells. Of the two lines which appear to separate the cone cells (*cl. con.*) from the rhabdomere (*rhb'm.*), the one nearer the axis of the ommatidium is the real line of separation; the other lies within the substance of the rhabdomere itself (compare p. 92).

" 62. A transverse section through a retinula proximal to the rhabdome and in the region of the hyaline cell. As in Figure 61, the pigment granules are drawn in only one of the retinular cells.

" 63. A transverse section through a single retinular cell in the region of its nucleus. The axis of nerve fibrillæ is represented by several small axes in the substance of the cell at one side of the nucleus.

" 64. A transverse section of the fibrous ends of the cells of one retinula in their passage through the aperture in the basement membrane. Each cell shows a well marked fibrillar axis, the centre of which is often occupied by a core of pigment. The basement membrane is viewed from its distal face. The irregularly oval body in the upper left-hand corner of the figure is probably a nucleus. It lies on the proximal face of the membrane through which it is seen.

" 65. A longitudinal section through the ommatidium of an advanced embryo. The numbers at the left of the figure correspond to the numbers of the six following figures of transverse sections, and indicate the levels at which the latter were taken. Figure 68 represents a section so nearly in the same plane as that shown in Figure 67 that its number has been omitted.

" 66. A transverse section at the level of the corneal hypodermis.

" 67. A transverse section through the distal end of a cone.

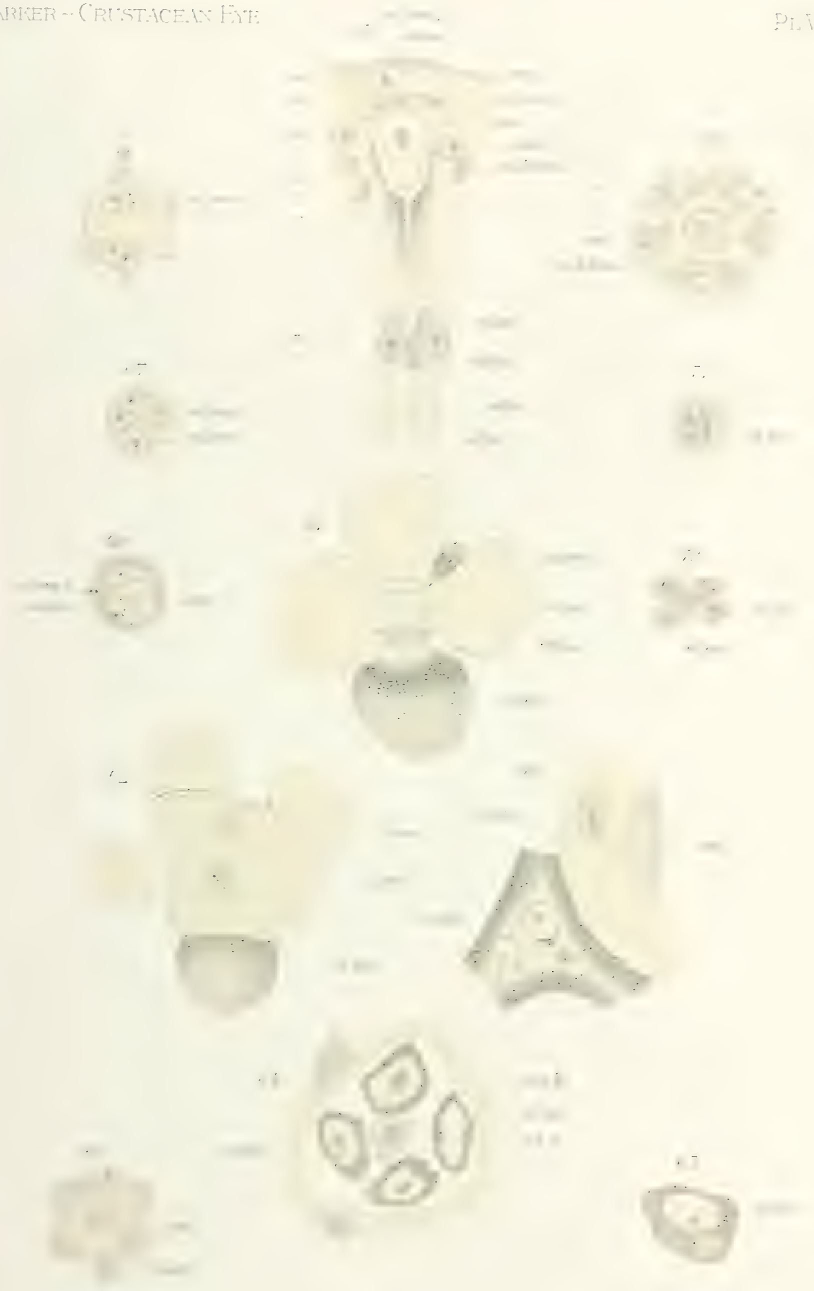
" 68. A transverse section made in a plane only slightly proximal to that shown in Figure 67.

" 69. A transverse section through the region of the distal retinular nuclei.

" 70. A transverse section through the proximal ends of the cones.

" 71. A transverse section through the retinula in the region of the rhabdome.

" 72. A transverse section at the level of the proximal retinular nuclei.



SEROLIS.

B. Meisel lith. Boston

PLATE VII.

Mysis.

Fig. 73. A longitudinal section of an ommatidium. The numbers at the left of the figure indicate the levels at which the sections for Figures 75–89 were taken. × 475.

" 74. The distal face of a corneal facet, cleaned in potash and examined in water. × 475.

" 75. A transverse section of three ommatidia in the plane of the corneal hypodermis. × 475.

" 76. A transverse section through the distal end of a cone. × 475.

" 77. A transverse section through the proximal end of a cone and the adjoining distal retinular cells. × 475.

" 78. A transverse section similar to that shown in the preceding figure, except that it is depigmented and stained in Kleinenberg's alum-hæmatoxylin. × 475.

Figures 79 to 82 inclusive represent consecutive transverse sections through the region of the proximal retinular nuclei of four adjacent ommatidia. The centre of each ommatidium is indicated by the group of cone cells (*cl. con.*), and the corresponding ommatidia in different sections are designated by the same Roman numeral. The nuclei around ommatidium II. have been numbered in Figures 79–81. Figure 79 represents the most distal section, and Figure 82 the most proximal one of the series.

Fig. 79. The bodies marked x and y are portions of nuclei the rest of which are correspondingly marked in Figure 80. × 475.

" 83. A transverse section of the four fibres at the distal end of the rod (compare p. 102). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 84. A transverse section of the rod at a slightly more proximal level than that shown in Figure 83. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 85. A transverse section of the retinula somewhat distal to the distal end of the rhabdome (compare Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 86. A transverse section from the region between the distal end of the rhabdome and the proximal end of the rod (compare 86 in Fig. 90). Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 87. A transverse section through the rhabdome and surrounding retinular cells. × 615.

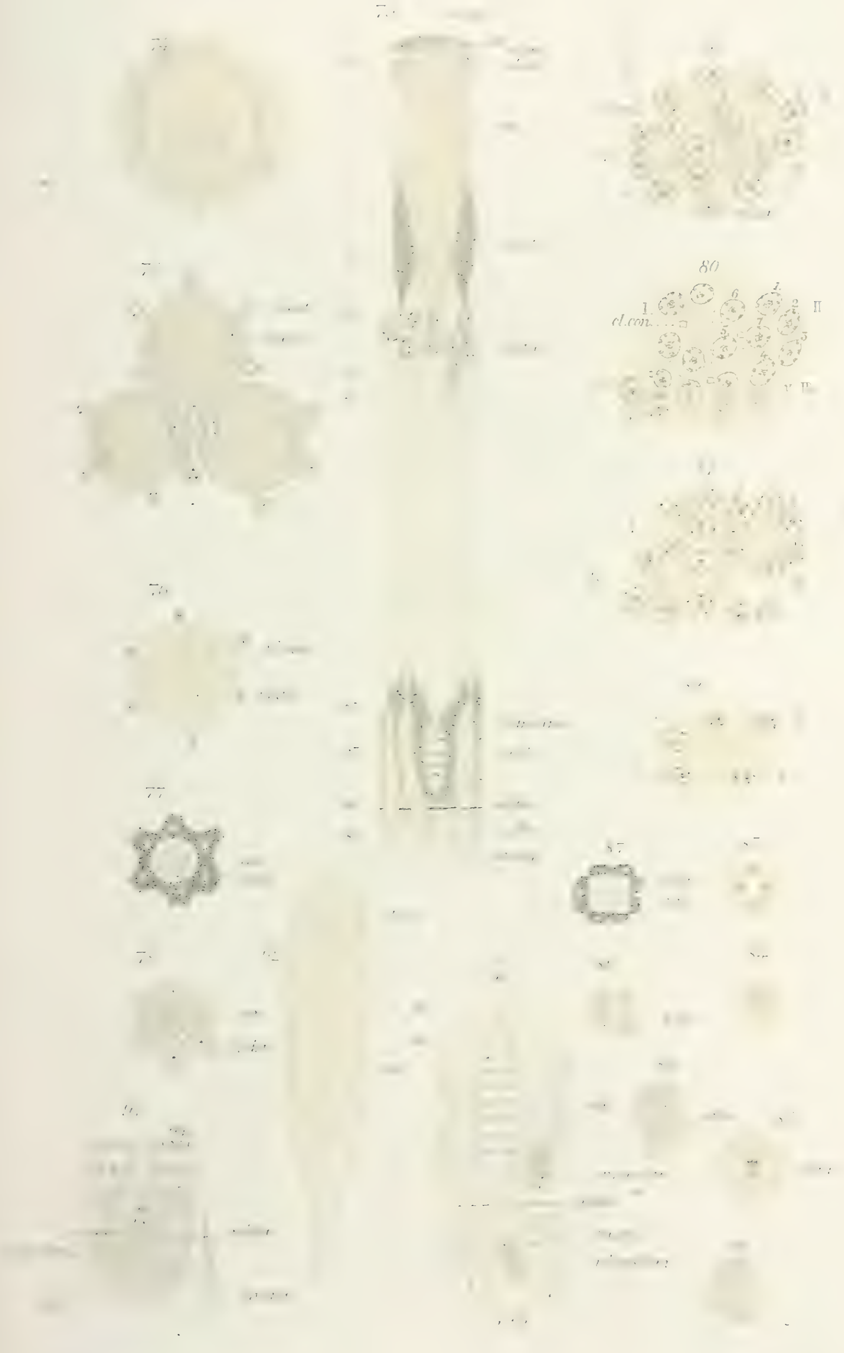
" 88. A transverse section, at the level of the basement membrane, through the nerve fibres from a single retinula. Depigmented, and stained in Weigert's hæmatoxylin. × 615.

" 89. A transverse section through the fibres of the optic nerve at a level midway between retina and optic ganglion. Preparation as in Figure 88. × 615.

" 90. A longitudinal section through the basal portion of one and parts of two adjoining ommatidia. Depigmented, and stained in Kleinenberg's alum-hæmatoxylin. × 615.

" 91. A section cut in the same plane as that shown in the previous figure, but including only the proximal ends of two rhabdomes. Preparation as in Figure 90. × 615.

" 92. A cone viewed from the side. Isolated in Müller's fluid and studied in water. × 475.


74
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II
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MYSIS.

B. Meisel lith. Boston

PLATE VIII.

Gonodactylus.

Fig. 93. Part of a tangential section through a superficial portion of the retina. The extreme edges of the section both right and left are immediately beneath the corneal cuticula; the central portion is farthest from the cuticula. At the right of the middle line are seen the ends of the larger ommatidia; at the left, those of the smaller. × 275.

" 94. A longitudinal section of a large ommatidium. The numbers at the left of the figure correspond to the numbers of six figures of transverse sections (Figs. 96–101), and mark the levels at which the latter were made. Depigmented. × 275.

" 95. A longitudinal section of a small ommatidium containing its natural pigment. × 275.

" 96. A transverse section through the cells of the corneal hypodermis and the distal end of the cone in a large ommatidium. × 275.

" 97. A transverse section through the distal part of a cone in a large ommatidium. × 275.

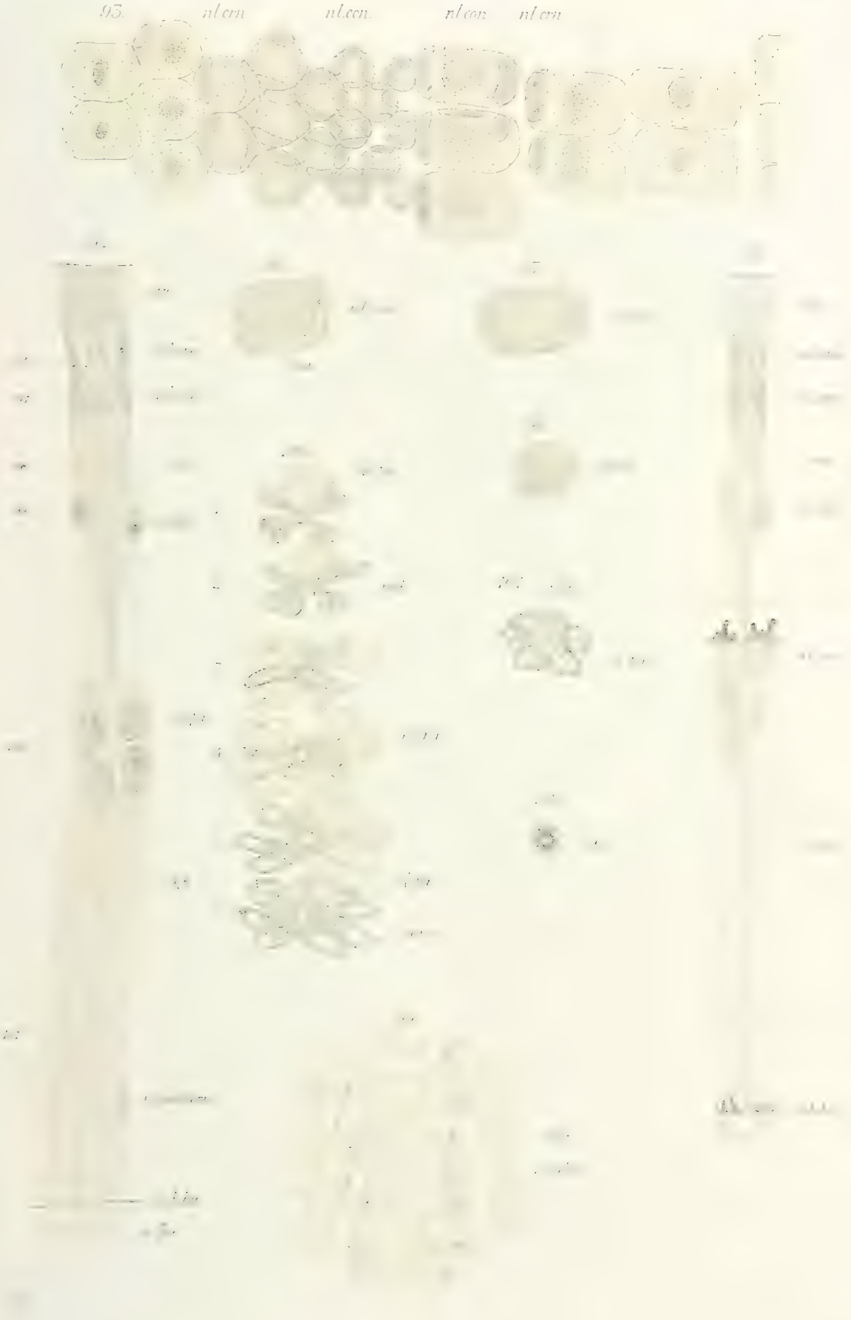
" 98. A transverse section through the middle of a cone from a large ommatidium. × 275.

" 99. A tranverse section through a number of cones at the level of the distal retinular nuclei in the large ommatidia. × 275.

" 100. A transverse section through six retinulæ of the large ommatidia in the region of the proximal nuclei. Each retinula is numbered. The plane of this section is slightly oblique, so that retinula 1 is cut at a relatively higher level than any of the others, and retinula 6 at the lowest level. × 475.

" 101. A transverse section of a retinula from one of the larger ommatidia, in a plane not far from the basement membrane. Depigmented. × 475.

" 102. A transverse section of a retinula from one of the smaller ommatidia cut in a plane nearly corresponding to that of Figure 101. × 475.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GONODACTYLUS.

B. Meisel lith. Boston

PLATE IX.

Palæmonetes.

In all Figures on this plate the magnification is 475 diameters.

Fig. 103. A longitudinal section of an ommatidium. The numbers at the left of the figure correspond to the numbers of nine of the following figures of transverse sections, and mark the levels at which the latter were taken.

" 104. A longitudinal section of an ommatidium which has been depigmented. The bodies marked x resulted from the action of the depigmenting reagent.

" 105. A facet from the corneal cuticula; cleaned in strong potassic hydrate, and examined from its distal side in water.

" 106. A transverse section through the region of the corneal hypodermis.

" 107. A transverse section through the distal end of a cone in the region of the nuclei of the cone cells.

" 108. A transverse section through the middle of a cone.

" 109. A transverse section through parts of four ommatidia in the region of the distal retinular nuclei.

Figures 110–112 represent three successive transverse sections, each through five ommatidia, in the region of their proximal retinular nuclei. Only the outlines of the nuclei and the five groups of cone cells (*cl. con.*) are drawn. The nuclei in each ommatidium are numbered from 1 to 7, and as their plan of arrangement is the same in the different ommatidia, corresponding nuclei have been designated by the same number. In some cases the nuclei were cut in two, and consequently appear in two adjoining sections. In such cases the two parts have been marked with the same number. Figure 110 is the most distal of the series; Figure 112, the most proximal.

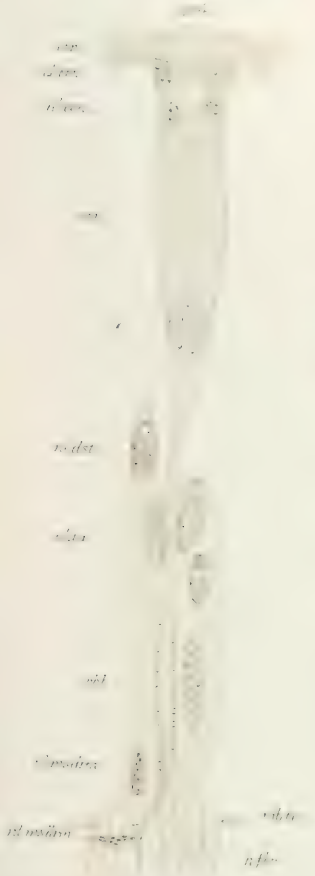
Fig. 113. A transverse section of the retinula near the distal end of the rhabdome. Depigmented.

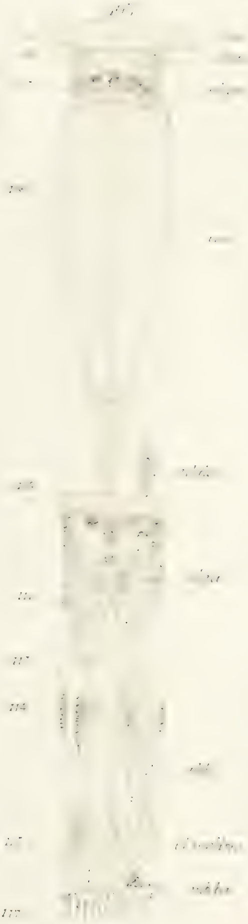
" 114. A transverse section of four retinulæ at the level of the eighth retinular nucleus.

" 115. A transverse section through four retinulæ in the region of the accessory pigment cells; viewed by *reflected* light. The retinulæ appear as dark masses embedded in a whitish field composed for the most part of the substance of the accessory pigment cells.

" 116. A transverse section through a retinula at about the same level as that shown in Figure 115. Depigmented.

" 117. A transverse section through the optic nerve fibres at a level slightly proximal to the basement membrane. Depigmented.





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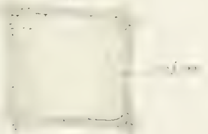

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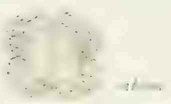

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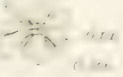

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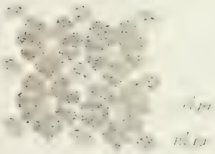

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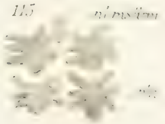

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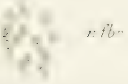

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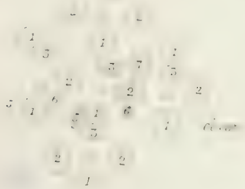

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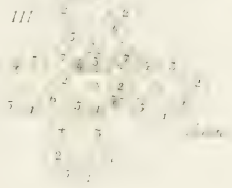

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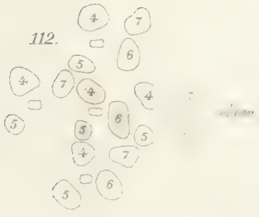
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G.H.P. del.

PALÆMONETES.

B. Meisel, lith. Boston

PLATE X.

In all Figures on this plate the magnification is 475 diameters.

Cambarus.

Figures 118–122 represent a series of five successive transverse sections through one and parts of four adjoining ommatidia in the region of their proximal retinular nuclei. Figure 118 represents the most distal section in the series; Figure 122, the most proximal. In these figures, only the outlines of the nuclei and the groups of cone cells are drawn.

Crangon.

Fig. 123. A transverse section through a number of ommatidia in the region of their distal retinular nuclei.

Palinurus.

Fig. 124. A transverse section through a retinula in its middle region. The outlines of the retinular cells cannot be distinguished; the position of each cell is marked by an irregular light mass in its centre.

" 125. A transverse section through a retinula in the plane of its eighth nucleus. Depigmented.

Cancer.

(Figs. 126–131.)

Fig. 126. A corneal facet viewed from its distal surface. The cuticula from which this facet was drawn was cleaned by being boiled in a strong aqueous solution of potassic hydrate. It was examined in water.

" 127. A transverse section of the distal end of a cone.

" 128. A transverse section through three ommatidia at the level of the distal retinular nuclei. The pigment granules have been indicated in only the lower circle of cells.

" 129. A transverse section through the distal region of four retinulæ. In the two on the right, the pigment granules have not been drawn.

" 130. A transverse section through a retinula near the base of the retina.

" 131. A slightly oblique section through the basement membrane. The upper part of the figure represents the retinulæ as seen in transverse section distal to the basement membrane; the part marked *mb. ba.* represents the region in which the membrane itself appears in section, and the lower half of the figure shows the cut fibres of the optic nerve. The pigment granules are omitted from the right side of the figure. The transition from the retinular cells to the nerve fibres is evident in passing over the section from top to bottom.

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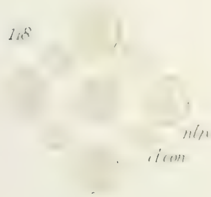

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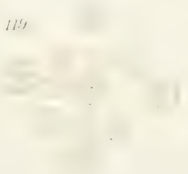

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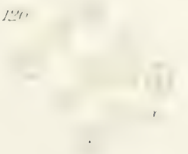

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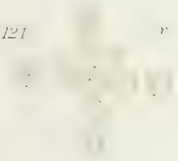

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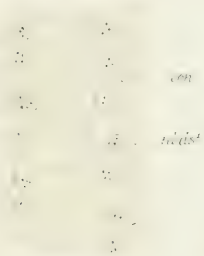

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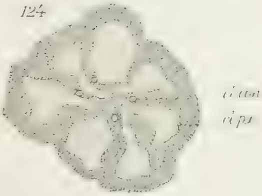

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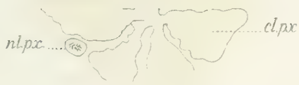

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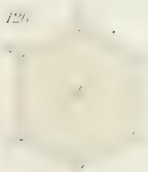

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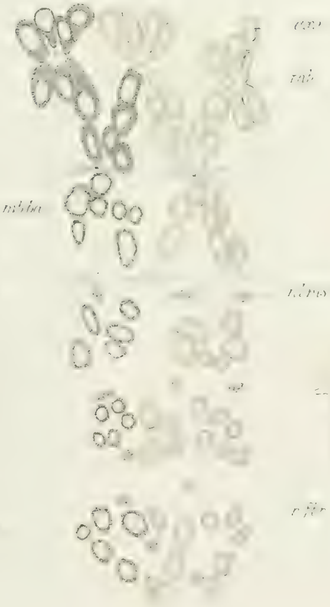
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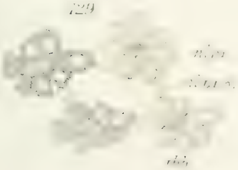

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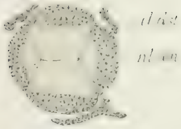
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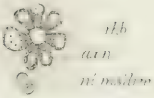

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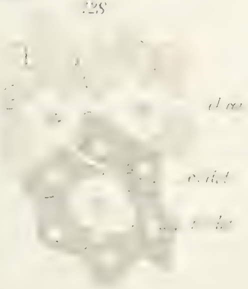

G.H.P. del. DECAPODA. B. Meisel, lith. Boston.

No. 3. — *On some Points in the Anatomy and Histology of Sipunculus nudus*, L. By Henry B. Ward.[1]

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I. Introduction.

Some two years ago, while working on Sipunculus nudus in the zoölogical laboratory at Göttingen under Prof. E. Ehlers, my attention was attracted by a peculiar organ in the region of the dorsal ganglion; and although it was a prominent feature of all transverse sections, no mention of its presence was found in the literature on Sipunculus. The observations made at that time interested me so much that the opportunity afforded by a short stay at the Naples Zoölogical Station last spring, for which I am indebted to the great kindness of Prof. A. Weismann and the Cultusministerium of Baden, was embraced to procure new, carefully preserved material. A study of the literature on Sipunculus revealed such lack of agreement between authors that a more general study of the form seemed likely to yield results, and, on the advice of Prof.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVI.

E. L. Mark, a more particular consideration of some moot anatomical and histological points was undertaken. This was unfortunately limited by the material on hand, which consisted merely of the anterior portion of the body, corresponding in general to the introvert of recent writers. As this contains, however, nearly all of the important organs of the nervous system to which especial attention has been paid in this paper, and as its separation from the rest of the body at the time of killing insured good preservation, it is hoped that the conclusions reached may not be without value, in spite of their incompleteness. The histological structure of the body wall and of the nervous system has been treated in detail, and from the results an attempt has been made to throw some new light on the systematic position of the Sipunculids.

METHODS.

The material used in these investigations was preserved with especial care, and every effort was made to procure a method of killing which should afford a clear idea of anatomical and histological relations under normal conditions, since many of the contradictory statements of various writers have been undoubtedly the result of studying specimens in a distorted state, due to muscular contraction, or have followed the examination of tissues poorly preserved. The thick impermeable cuticula, and the wealth of muscular tissue in the body wall, render it a difficult matter to avoid at the same time both evils. The method finally adopted as yielding the best results is as follows.

After remaining some time in clean sea-water to clear tentacles, body wall, and œsophagus of adhering sand, the animals were brought into a shallow dish of sea-water, and 5% alcohol was allowed to flow gently over the surface, forming thus a thin film, which disseminated itself gradually, and produced in the animals a complete relaxation of the body muscles. It did not seem to answer equally well when the alcohol and water were mixed at the start, as has been recommended for some animals. The length of time necessary for the attainment of complete narcosis cannot be exactly given. It varies greatly with different individuals; but if, after lying some four to eight hours, the animals make no contractions on being gently probed with a dull instrument, they may be regarded as sufficiently stupefied, and transferred to 50% alcohol. After a short stay in this, the introvert was cut off, and this alone subjected to treatment with higher grades of alcohol, which insured the penetration and consequent good preservation of the tissues. The only point in the process which requires especial care, and which often produces a disappointing failure, is the transfer from the salt water and its added alcohol to 50% alcohol. If the animal is but partially narcotized, the muscular contraction induced by the transfer will spoil the specimen. If, on the other hand, it be left too long, the weaker parts of the body wall, especially the upper smooth zone of the introvert, swell out quite rapidly (through osmosis?), and not only the external form but the histological elements as well are badly distorted. The golden mean between these two extremes yields specimens as excellent for histological work as for the study of external relations. Material preserved in this way may be well stained by all methods. Where any stain has been of especial value in the study of particular organs or tissues, it will be noted under the topic in question. In this place I wish to express my thanks to Prof. E. Ehlers of Göttingen and to Prof. A. Dohrn of Naples for past favors, and to Mr. A. Agassiz, Prof. E. L. Mark, and Prof. E. B. Wilson for more recent kindnesses in supplying me with material for this study.

II. External Anatomy.

Selenka ('83, p. 92) has given a full description of the external characters of *Sipunculus nudus.* There are however numerous points of interest which first appear in a well expanded specimen, and which deserve especial attention. The body consists of a large posterior region covered by the quadratic integumentary areas (Hautfelder) and of a portion anterior to these, which is called the introvert.

1. Introvert.

This includes on the average one sixth of the entire length of the animal, and has in general the shape of a truncated cone (Fig. 1), the anterior base of which, only a little less in diameter than the posterior, is surmounted by a wreath of tentacles which nearly encircle the mouth. This region is ordinarily found entirely, or for at least two thirds of its length, invaginated into the following portion of the body, and is only rarely seen extended. In the latter condition it measures from three to four centimeters in length. The circular muscle bands, which are separate in the posterior part of the body, are here fused into an unbroken sheet of muscular tissue. The fusion takes place abruptly, and causes the immediate cessation of the integumentary areas (Hautfelder) due to the banded musculature, thus fixing a definite posterior boundary to the introvert. On the latter one can distinguish (Fig. 1) four regions:

(1) a posterior papillate zone[1] (*z. pap. p.*), (2) a smooth zone (*z. lev.*), (3) an anterior papillate zone (*z. pap. a.*), and (4) the tentacular crown (*pli. ta.*).

The posterior papillate zone occupies the posterior half of the introvert, and shows a posterior portion, which is thickly studded with papillæ, and is dark brown in alcoholic specimens, and an anterior part much lighter in color, where the papillæ are somewhat scattered. The lighter, almost translucent appearance of the anterior portion of this zone, which permits the central mass of the œsophagus and retractors to shine through as a dark band, is due to the great diminution in thickness of the muscular layers. The line of demarcation between the lighter and darker portions of this zone is somewhat definite, and is marked internally by the fusion of the longitudinal muscles into a continuous sheet, and by the entrance into the body wall of the first large composite nerve given off from the ventral nerve cord (*cf. infra*).

The papillæ of this region are all shaped like the bowl of a spoon with the concavity directed toward the body and the tip posteriad. Adjacent to the integumentary areas they are closely crowded, and overlap like the shingles of a roof, so as to hide the skin completely. They vary in size and shape, but are in general broadly pointed, measuring on the average .25 mm. in length, and .65 mm. in breadth.[1] Passing forward, this general form is preserved until the point of transition from the dark to the light portion of this posterior papillate zone is reached. Here the papillæ grow abruptly smaller in absolute size, though relatively longer and narrower, until the characteristic mammiform papilla of the light region is reached. These only are represented in Figure 1. They are much lighter in color, and much less crowded, than the posterior papillæ, and leave irregular patches of skin entirely free. In breadth such a papilla measures .25 mm.; in length, .37 mm. I am unable to confirm the statement of Andreae ('81, p. 205), that they are arranged "in gleichen Abständen"; for the relative distances are extremely variable, being from 70 to 300 μ in the anterior portion of this zone. I was also unable to find the arrangement in a double spiral reported by Vogt und Yung ('88, p. 381). There seemed to be in fact no regular arrangement common even to a majority of the specimens examined.

Passing forward, the papillæ grow ever sparser, and finally terminate along a well defined line, which marks the beginning of a smooth zone (*z. lev.*, Fig. 1) entirely free from papillæ. It measured 7 mm. in breadth in a specimen which had an introvert of 4 cm. total length. Anterior to this is a zone (*z. pap. a.*) with small papillæ; this measured 3 mm. in breadth in the same specimen. The papillæ of this zone appear superficially as minute discoidal elevations of the skin. In well expanded specimens, the tentacles droop over and nearly cover this zone, which is not separated from their base by any definite line, since the papillæ extend forward a short distance over the aboral surface of the tentacles, becoming gradually less frequent. They are indeed met with occasionally on the whole of this surface, but are entirely wanting on the oral aspect of the tentacles. In all well expanded specimens these regions are as well defined as in the one which has served as the basis for this description, and the zones have the same relative size as in the measurements given.

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[1] The posterior half of the posterior papillate zone is not shown in Figure 1.

2. Tentacular Fold.

The tentacles (Tentakelmembran) originate in the larva as two folds of the oral margin, — "lippenartige Falten," Hatschek ('83, p. 115), — separated dorsally but continuous ventrally, and lying right and left of the median line. Starting, then, from this primitive condition, the form found in the adult would be reached, if it be supposed that these flaps of skin are plaited radially to the oral centre, and that the growth is more rapid on the oral surface as well as toward the margin, thus necessitating a reflection of the flaps back upon the aboral surface. For a careful examination shows that in well expanded specimens the so-called tentacles consist of a thick fold of skin surrounding the terminal oral orifice with numerous plaits and folds arranged radially. This continuous flap may be called the tentacular fold, in preference to membrane, since the latter suggests a false idea of its nature, and its subdivisions may conveniently be termed the radial plaits.

The general form of the tentacular fold, as viewed from above (Fig. 2), may be said to be that of a horseshoe with the smaller dorsal curvature interrupted on the middle line. The external or ventral semi-circumference is reflected over the superior portion of the introvert, whereas the internal or dorsal portion makes a ventral flexion over the mouth, and lies higher than the other half of the tentacular fold. The superior height of the dorsal portion of the flaps in the larva caused Hatschek ('83, p. 115) to regard this as the "Anlage" of the first pair of tentacles. He knew nothing, however, of the further development of this portion, which probably represents the origin of the dorsal horns, since separate tentacles do not exist. In the adult, at any rate, this region shows two horns (Figs. 1 and 2, *crnu. d.*) projecting ventrad over the oral aperture, and forming together the dorsal curve of the horseshoe. Brandt ('70, p. 22) assigned a horseshoe shape to the crown of tentacles, but this has been declared false by later investigators.

This normal hippocrepian form is often distorted when the introvert is only partially extruded, or when there is undue muscular contraction within the soft mass of the fold itself, and it is always more or less disguised by the secondary radial plaits into which the fold is thrown. The relation of these parts will be easily understood by comparing Figures 1, 2, and 3. It will thus be seen that the reflection of the tentacular fold, with its deep radial plaits, brings into prominence regions — the "triangular tentacles" of some writers — which alternate with retreating portions, so as to impart to the margin the appearance of being cut or toothed, especially if the contraction of the muscular elements in this soft fold has drawn it somewhat out of shape. In fact, the description uniformly given by systematic writers has represented the tentacles as a membrane with numerous marginal incisions. This error is due in part to distorted specimens; the true form may be said to be crenate.

Therefore one can speak of the formation of tentacles only in a general sense. But the fold may be regarded perhaps as the simpler form, from which, by the development of certain areas alternating with regions of reduction, the more highly specialized digitate tentacles might be developed. Only the main folds are represented in Figure 2. These may be much complicated by the appearance of subordinate plaits, until the general plan is confused by a mass of detail. The more simple forms proved, on microscopic examination, to have been the most successfully killed, in that the muscular elements were in a more perfectly relaxed condition. The aboral surface of the tentacular fold is concave, except in the dorsal horns, where it is convex; it has the same radial folds as the oral surface with which it is approximately parallel. Numerous low circular ridges traverse the aboral surface, and bear in varying number the small papillæ already mentioned. These ridges are not regular in course or size, and evidently vary with the convexity of the tentacular fold. In the midst of these, on the dorsal median line, can be found on careful examination a small oval opening (Figs. 2, 3, *can. o. ceb.*). It is often so hidden in the ridges of the aboral surface as to make its discovery a matter of some difficulty. The opening measures about 1 by 0.5 mm., with its long axis transverse, and is surrounded by an evident marginal ridge. This is the opening of the canal of the cerebral organ, to be described later.

III. Histology.

1. Body Wall.

In the body wall may be found the following layers, beginning with the surface : (1) a cuticula, (2) a hypodermis, (3) a cutis, (4) the muscular system, covered internally by (5) a delicate peritoneal membrane.

a. *Cuticula and Hypodermis.*

The cuticula consists of a substance optically like chitin, but differing from this, as has often been pointed out, in being soluble in boiling KOH. It is further aberrant in the absence of cellulose, which has been shown by Ambronn ('90) to be characteristic of true chitin. Tests with chloriodide of zinc showed neither any trace of blue nor the subsequent pleochroismus described by that author for true chitin. This layer is undoubtedly the product of the underlying hypodermal cells, which are everywhere found in a single layer, and normally display a sac-like form, although, as mentioned by Vogt und Yung ('88, p. 383), they may by contraction or compression of the body wall be drawn out into the form of spindles. This has given rise, as they mention, to the erroneous interpretation of such groups of elongated cells as being sensory organs. In contradistinction to these authors, I do not find the proximal ends of these cells ordinarily continuous with fibres which extend to the muscular layer, and cannot agree with them in regarding the entire mass external to the muscles as one layer. For if one examines a transverse section of the body wall as seen in Figure 5, the majority of the hypodermal cells are seen to be clearly marked off from the underlying tissue by the cell wall. The fibres of this subjacent tissue, to be described later, often extend up to the bases of the hypodermal cells ; but close examination in favorable regions shows the connection to be merely apparent. Often when these cells are crowded and distorted by near-lying glands, one is inclined to believe in an actual continuity of cell and fibre which cannot be demonstrated, and which, so far as I could find, is not present in less confused regions.

Lying partly in the hypoderm, but mostly below it, are the dermal bodies (Hautkörper), which are of three sorts. A description of these will be given in the account of the cutis, with which they are most closely associated. No further specialized cells of any kind were found, neither sensory cells nor peculiar nerve endings of any sort, and I am inclined to regard the claims of their presence as founded upon the examination of poorly preserved material. Several times it was observed that delicate filaments, branching from some nerve fibre of the skin, proceeded to the hypodermis and penetrated apparently undifferentiated cells; certainly the distal surface of these cells bore no sensory hair or bristle. But the exact manner of termination of the nerve filament remained in doubt.

b. Cutis.

In placing a cutis in the list of the layers of the body wall, I am not unaware that the two most recent publications on Sipunculus deny its presence. As already mentioned, Vogt und Yung ('88) regard the entire extra-muscular layer as hypodermal, while Andrews ('90) evidently discredits the existence of a cutis by omitting the name altogether. What, then, is the actual condition of affairs? In sections one finds (Figs. 4, 5) between the hypodermis and the muscular layers a mass of gelatinous tissue, traversed in all directions by fibres, and containing not only glands of various sorts, but nerve fibres and pigment cells as well. Thus, though varying greatly in thickness in different regions of the body, it may properly be regarded, in the light of the characters mentioned, as a true cutis. The principal part of this layer is the connective-tissue jelly, homogeneous in its consistency and forming the matrix in which the nerves and dermal bodies lie. It is traversed in all directions by a multitude of the finest connective-tissue fibrils, which anastomose but rarely. Occasionally a minute nucleus can be observed in the course of a fibre. Scattered nuclei of a larger size, connected with nerve fibres or amœboid cells, are not infrequent in this mass, and have been erroneously regarded as belonging to the connective tissue. Irregular amœboid cells with but one nucleus and of a different refractive index from the general mass are found, sometimes in considerable numbers, and are perhaps similar in nature to the leucocytes of the tentacles, to be described later.

c. Pigment Cells.

Besides these elements one finds multinuclear cells of irregular outline more or less filled with granules of a highly refractive character. These are the pigment cells, so characteristic of this group that they deserve special consideration. Andreae ('81, p. 209) has given almost the only description of these peculiar structures. He represents the pigment granules as closely packed in meshes of connective tissue on which nuclei may be observed. This appearance is no doubt due to poorly preserved material; the true nature of the cells, as well as the process of deposition of the pigment, can clearly be understood from a section such as is shown in Figure 5. The cutis contains here a group of irregular amœboid (?) cells, distinguishable from the surrounding mass by their refractive power, and containing from five to many deeply stained nuclei $3\,\mu$ in diameter. The cells are all without any proper membrane, though often surrounded by an envelope of connective fibres, and enclose a varying number of highly refractive granules distinguished by indifference to any coloring matter but picric acid, which they take up with great avidity. Their natural color by transmitted light is a greenish yellow; by reflected, however, a dull brown or yellow. That the process of formation is gradual becomes evident on the examination of a section like Figure 5. In some cells are seen only a few such granules, or they are confined to one part of the cell; and all stages are present from this up to a mass of closely packed granules in which neither cell plasma nor nuclei are visible. Even in such cells the nuclei could be demonstrated by prolonged staining and thin sectioning. The plasma of these cells shows at first some slight affinity for hæmatoxylin, which disappears as the granules become more crowded. In the first stages of deposition the granules are mere bright dots too small to be measured; in the more thickly crowded cells they have reached often twice or thrice the size of a nucleus, and alongside of these are also granules as minute as those of the earlier stage. Such cells are present not only in the cutis, but also in all other organs of the body. They are not always as numerous as shown in Figure 5; in the tentacles they are quite rare, whereas the nervous system contains especially large numbers in all its parts. Somewhat similar cells were found by Bürger ('90) in the nervous system of Nemertines. Wherever these cells are found in Sipunculus they display the same structure, except that elsewhere than in the cutis they are only found well filled with granules. Whether a migration actually takes place, as is suggested by their evidently amœboid character, I was unable to determine. It is to the presence of large numbers of these cells that the papillæ of the posterior zone and the walls of the cerebral canal owe their dark color. The pigment cells are present in much greater numbers in large than in small specimens, i. e. in older than in less mature ones. I can confirm the statement of Vogt und Yung ('88, p. 386) that fasting rapidly decreases their number. It is not a necessary conclusion that this is to be regarded as reserve material. For even waste may, under the pressure of failure in the food supply, be drawn into the system and worked over again.

d. Dermal Bodies.

Various opinions have been held by different authors as to the morphological value of the dermal bodies. Keferstein und Ehlers ('61) described them as glands, Leydig ('61) regarded them as sensory organs; but later writers have inclined to the former view. Andreae ('81) described three varieties of these organs, whereas Vogt und Yung ('88) made the claim that the sensory organs, Andreae's third variety, do not exist, and that all of the glands are merely modifications of one sort. As to the first statement, they are undoubtedly correct; but to the latter view I am unable to assent. The transition from one sort of gland to the other, though plausible from surface views such as given by those authors, is only apparent. For if one examines carefully prepared sections, the seeming similarity gives way to a well marked difference. Not one of the glands is actually unicellular, as claimed by Vogt und Yung, and the multicellular contain never less than five cells, which serves to separate them clearly from the other kind, which is always bicellular. Moreover, their behavior toward staining fluids is very different. For while the bicellular glands take up hæmatoxylin with such rapidity as to become almost black in a few seconds, the multicellular are but little affected by this reagent. Carmine solutions stain the two about equally, but bring out the nuclei, which are invisible in a hæmatoxylin stain. And, finally, the morphological elements of the two sorts are essentially different, as will be shown. The old classification of bicellular and multicellular glands will therefore be retained, and the structure of each will be examined more in detail.

The *bicellular glands*, when viewed, even in the living animal, directly from above, display a clear zone along the line of the partition wall between the cells. This is invisible if the gland be viewed from the side, or at a considerable angle, and gives rise to various images if the line of sight be more or less nearly perpendicular to the surface. As the papillæ which contain the glands have sloping sides, never exactly alike, it is easy to understand how views of the glands from many different directions may be had from a surface inspection, and how the various images may give the appearance of a series from the bicellular to the multicellular gland. If one examines, however, sections of the skin perpendicular to the surface (Figs. 4, 5), the bicellular glands appear at once as a distinct type. Ordinarily spherical, they may often be found mutually flattened where several lie closely pressed together. They vary in diameter from 40 to 50 μ, and present very different appearances according to the stain employed. The greatest number of structural details are obtained from those lightly stained with hæmatoxylin. Sections thus stained are represented in Figures 6, 7, and 8. Though evidently differentiated hypodermal cells, they lie almost entirely in the cutis, enveloped by a delicate coat of connective tissue, in which can be found occasional flattened nuclei. The distal half of each cell is occupied in great part by a large vacuole, directly continuous with that of the adjoining cell. The space thus formed measures $12 \times 15 \times 25\ \mu$, and communicates with the exterior by means of a narrow canal opening simply on the surface of the cuticula. The duct measures 6–8 μ in diameter, and at the distal end of the cell does not lie in the centre of the neck (Fig. 9). The connective-tissue envelope does not penetrate between the cells, which in consequence are separated *only* by their own membranes (Fig. 6 or 11,*), and these, continued over or under the distal vacuole, appear, if the cell be viewed along the plane of the partition, to bisect the vacuole (Figs. 6, 10); the latter suffers, however, a slight constriction along this line, so as to impart to it in transverse section a biscuit-shaped appearance (Fig. 7). Its longitudinal section is cordiform, as shown in Figure 6. The two large clear spherical nuclei, 9 μ in diameter (Figs. 10, 11), may be differentiated with carmine or saffranin, and then appear in the lower half of the cell, usually nearly symmetrical to the dividing membrane. Each displays a single central deeply stained nucleolus, and many minute chromatine granules. If the plane of the section pass transversely *below* the vacuole (Fig. 11), the cells are seen to possess a hemispherical form, and the dividing membrane to make an S-shaped curve.

Whether active or resting, a clear zone of plasma forms the periphery of the cell on all sides, and is therefore adjacent to the vacuole, as well as to the external surface of the cell. This zone is traversed radially by delicate fibrils, the beginnings of the plasma reticulum which fills the cell, but which ordinarily is easily seen only in this clear zone. In every section one finds a few cells of this sort, which, besides an empty vacuole, exhibit this reticulum very plainly throughout the entire faintly tinted cell body (Fig. 8).[1] They are evidently the functionally inactive or resting cells. The first stage in secretion is seen in the accumulation of numerous granules in the basal portion of the cell (Fig. 6), which are stained deeply with hæmatoxylin, and by continual aggregation finally obscure the reticulum, and impart to the entire cell, save its marginal zone, an appearance almost opaque (Fig. 7). The secretion first appears in the vacuole in the form of minute beads at the peripheral ends of the reticular fibrils which traverse the clear zone and terminate at the edge of the vacuole each in a single bead (Fig. 7). During the formation of the secretion in the vacuole, the mass of opaque granules moves toward this space; and the close of the process is represented in Figure 8, where the vacuole is filled with a homogeneous mass, displaying in a somewhat lesser degree the affinity for hæmatoxylin stains which characterized the granules while contained in the cell substance itself. At the same time, these granules have disappeared, except a few which are grouped in a zone about the vacuole; and the cell has become thereby so much lighter as to show the reticulum at its proximal end.

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[1] Strictly speaking, Figure 8 represents the *last* phase in secretion. The first differs only in the absence of matter in the vacuole, and of the few granules just below it.

This description of the activity of these organs would seem to place their glandular nature beyond question. In comparing the two sorts of glands, it is of great importance to note that the cells do not show in this case any connection with nerves, whereby they are sharply distinguished from the multicellular glands. The space (Spalt) which Andreae ('81, p. 215) describes as existing between the cells of these glands was found not infrequently in some preparations, but it is evidently due to shrinkage. The double membrane separating the cells, described by the same author, was probably produced in the same way.

The distribution of these glands is peculiar. Over the general surface of the body they are found only rarely, and on the introvert they are present only *in the papillæ*, the interspaces being entirely free from them. Each papilla of the posterior zone of the introvert shows in surface views an irregular double or triple row crossing the convex outer surface near the base, and occupying one half to one third of its entire breadth. Rarely isolated bicellular glands are found near the tip. This regular limited distribution allows perhaps a conjecture as to their possible function. Inasmuch as the behavior of the secretion toward coloring reagents would seem to mark it as mucine (cf. Hoyer, '90), may it not be that these glands furnish the lubricant demanded by the constant movements of the two walls of the introvert? The papillæ are especially affected, of course, rubbing against each other in the constant inversion and eversion. They receive, furthermore, the greater part of the pressure as the animal forces its way through the sand, in the method described by Andrews ('90, p. 391). The animal does not advance backward with the "Eichel voran," as maintained by Andreae ('81, p. 220)! The secretion may also be of use in cementing the sand grains into a sort of tube noticeable when the animals are dug out of the sand.[1]

The *multicellular glands* present a type easily distinguishable from that just described. They are to be met with everywhere, not only in the papillæ, but lying in the interspaces as well, and extending up into the clear zone of the introvert, where they are the only differentiated hypodermal cells. Never much crowded, they become here sparser, until they completely disappear at the level of the upper papillate zone; nor are they to be found in or above this zone, nor at any point on either surface of the tentacular fold. The multicellular glands may be identified on surface preparations, but an insight into the histological relations is first afforded by sections. With hæmatoxylin the cell body stains lightly but uniformly, the mass at the distal end more deeply (Fig. 12), but with this stain no nuclei can be found either in the cells or in the connective-tissue investment of the gland. Each gland is seen to be made up of a number of flask-shaped cells, which are separated by thin partitions and which unite at their distal ends into a duct piercing the cuticula and opening upon its surface to the exterior. Andreae ('81, p. 216) was unable to find any nuclei in these cells. The application of a carmine stain, however, shows their presence near the proximal ends of the cells (Fig. 14), where they often lie flattened against the cell membrane by the crowding of the granules accumulated in the cell plasma. The same stain demonstrates also (Fig. 13) smaller nuclei at various points in the connective-tissue investment. There is likewise seen to be a difference in the cells of any one gland which indicates alternation in secretive activity. Thus the plasma of some cells is thickly crowded with large granules, which are entirely wanting in other cells. This is most clearly demonstrated in a transverse section of the gland, as shown in Figure 13. The cells differ in intensity of color to correspond with the number of granules present, and large distended cells are found near those which are evidently thinner and poorer. The product of these glands is a substance more waxy than fluid, to judge from its manner of caking in the duct, and breaking up into small fragments, like sebaceous material. Its discharge is evidently gradual like its production; for I have never found a gland empty, nor does the total amount of secretion present vary greatly. This alternation in functional activity between the various cells of one gland and the constancy of secretion from the gland as a whole stand in strong contrast with the resting and active stages in secretion as found in the bicellular glands. The function of the secretion from the multicellular glands is probably more general, since the glands are so uniformly distributed over the surface of the body.[1]

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[1] For this suggestion, and the observation that such a tube exists, at least for S. Gouldii, I am indebted to my friend, Mr. C. B. Davenport.

One of the most peculiar points in connection with these glands is their relation to the nervous system. In almost every instance, a nerve fibre can be clearly traced from the subdermal plexus to the proximal end of the gland, and on fortunate sections (*gl.''' n. fbr.*, Fig. 14) it was possible in a number of cases to demonstrate an actual connection between gland cell and fibre, in that the former was prolonged into a delicate fibril, which, passing out from the glandular cavity in company with similar fibrils from the adjacent gland cells, entered within the neuroglia into the substance of the nerve and appeared to make up its fibrillar structure. This connection of gland cell with nerve fibre is found in all regions of the body, and is not confined, as Andreae maintained, to the posterior tip (Eichel) of the animal. In spite of this direct nervous connection, there seems to be little ground for regarding these structures as sensory organs, the interpretation put upon them by Leydig ('61) and others after him. A careful examination brought to light only the single kind of cells, which are in no way comparable with sensory cells. On the other hand, it may be said that a rich nervous supply is not without parallel for glandular structures.

The capsules of these glands are very thick, and nuclei are found on the partitions between the cells, showing that each cell is enclosed in a separate investment. But the partitions are never as strong as the general sheath of the entire gland, which possesses nearly the optical appearance of muscular elements. The variations in size are so great, being from $40 \times 50\,\mu$ to $90 \times 150\,\mu$ in the same region of the body, that the probability of a muscular capsule suggests itself strongly.

Allusion has already been made to the relation of the glands to the papillæ. In each papilla of the posterior zone, one finds at its tip an indefinite crowded mass of multicellular glands, and in an irregular double or triple row across the basal half, the bicellular variety. All of these open upon the external convex surface of the papilla. That the relation of glands to papilla is an intimate one, first appears clearly from the formation of the latter. As it is evident that new papillæ must be added with the growth of the animal, it is of interest to note the steps in the formation of these structures. The first indication is an evident crowding of the otherwise scattered multicellular glands in the centre of some interspace of more than average size. Then the bicellular glands make their appearance as a loose double row, and so quickly that no intermediate stage could be found. They grow more crowded, and soon after their appearance a shallow furrow may be seen to enclose the mammiform area which they occupy. The skin seems to be tucked in on the three sides at once, and as the furrow grows deeper the papilla becomes more and more prominent. The growth in any papilla is increase in breadth rather than in length, so that the relative dimensions gradually change, and the older papillæ in any region are markedly wider than those more recently formed, while the length remains nearly constant throughout the entire zone.

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[1] See Addendum.

Sense Papillæ. — The papillæ of the anterior zone are thickenings or modifications of the hypodermis, rather than typical papillæ like the posterior ones; they correspond probably to the "Wimperdrüsen" of Vogt und Yung ('88, p. 406). They are externally marked as small rounded prominences of the skin, varying in diameter from .15 to .40 mm., and often exhibit an oval or dumbbell-shaped opening in the centre of the prominence. Viewed in cross section (Plate II. Fig. 18) they display an evenly rounded contour, which is surmounted by cilia. These are short on the lateral margins of the area, but increase in length as they approach the apex, where they are longest. If one notices the basement membrane, here for the first time well developed, it will be seen that the prominence is almost entirely due to the increased height of the hypodermal cells, which have changed their form from that of the usual hypodermal elements so as to assume the character of filamentous cells, such as compose the hypoderm of the tentacles, with which they are identical. The isolated elements of the latter (Plate II. Fig. 21) might, indeed, answer equally well as types of these cells. In addition to the elongated nuclei of these cells, some few rounded ones are seen scattered between the filamentous cells, more usually near the basement membrane. Perhaps more common than the normal expanded form of the papillæ, just described, is the retracted condition shown in Figure 17. Such are found in all degrees of contraction, alternating irregularly with the normal form. The papilla figured is perhaps fully retracted, and one notes that the apical area lies sunk in the structure, so as to give the effect of a cavity and a duct. That this is due in part to the contraction of the cells themselves, and in part to the retraction of the central portion of the papilla, is clear from a comparison of Figures 17 and 18. In spite of this, I was unable to identify any muscular elements connected with the organ, the many fibres which are attached to the proximal side of the basement membrane being, in refractive power and other optical properties, and in the character of their nuclei, indistinguishable from the other cutis fibres. One often finds such an appearance as is given in Figure 16. This is evidently a tangential section of a similar organ; the central clear space represents the hollow produced by the retracted apical area, and the apparently round nuclei are merely the elongated forms transsected. The appearance of the cells suggests no glandular nature, and nothing could be found resembling a secretion. For this reason I am inclined to question the propriety of the name "Wimperdrüsen" (Vogt und Yung, '88, p. 406), and to regard them as simple sensory organs. The retraction of the apical area would then be a simple method for protecting the long and delicate cilia during the advance of the animal through sand, similar to that reported by other observers for such organs in various groups. I was unable to discover any nerves connected with these organs, so that their sensory nature remains unproved, although none the less probable (Eisig, '87, p. 548). The structures just described are distributed over the aboral surface of the tentacles in somewhat irregular lines, becoming less frequent toward the margin of the fold, but are not present on its oral aspect. They suggest strongly the diffuse sensory organs (Becherorgane) of Capitellidæ, described by Eisig ('87, p. 547), but they are certainly less highly differentiated in the following respects: — 1. The cilia are not confined to the apical area (Polfeld), but are more or less diffused over the entire prominence. 2. There are only a few of the nervous nuclei (Körner) present in the basal portion. These structures recall the cup-shaped organs of Capitellidæ most strongly in the character of their elements, the filamentous cells, in their relation to the general hypodermis, and in the thin cuticula which covers them. In both cases, connection with nervous elements remains a matter of conjecture.

Very similar organs have been described by Spengel ('80, p. 465) for Echiurus, as appears at once from a comparison of the figures given by that author (Taf. XXIV. Figs. 21, 22). These, however, differ materially from those in Sipunculus in two respects: first, no cilia were present (Spengel believes them to have been lost through poor preservation); secondly, a fact of more importance, a large number of unicellular glands are found immediately below and in connection with these organs in Echiurus. The latter are certainly not present in Sipunculus. The distribution of these organs is quite different in the two forms, since there occur from one to seven on each of the papillæ of Echiurus, whereas in Sipunculus they are confined to the small anterior zone of the introvert.

e. Muscular Layers.

Of the muscular layers the diagonal is not present in the introvert. The circular layer, which is banded throughout the rest of the body, fuses at the end of the integumentary areas into one continuous sheet, and grows gradually less important anteriad, being almost entirely wanting in the anterior zones. The longitudinal muscular bands do not fuse until the middle of the posterior papillate zone is reached. From this point anteriad they also become reduced so that in the smooth zone the entire muscular layer measures but 70 to 90 μ in thickness. This remnant passes over into the retractors in a manner to be described in treating of the tentacular musculature.

2. TENTACULAR FOLD.

A cross section of the tentacular fold shows that it consists of two layers of skin, which form the oral and aboral walls of an irregular cavity, traversed perpendicularly by numerous trabeculæ binding the two sides together (Fig. 3). This cavity is the extension of the so-called blood system, and is often found more or less filled with a coagulum. The character of the oral and aboral walls of this cavity differs: the structure of the oral portion will be considered first.

a. Oral Wall.

The cuticula (Plate III. Fig. 23) is extremely thin, never exceeding 2 μ, and usually appearing as a fine double contour. It is pierced by many pores for the exit of the fine cilia, which cover this surface from the apex of the fold down into the mouth. Evidently the inversion of surfaces in the retracted condition of the introvert led Selenka ('83, p. xvii) and others to regard the oral surface of the tentacles as without cilia, and to maintain that the aboral surface was ciliated, exactly the reverse of which is true.

The hypodermis (Plate III. Fig. 23) is composed of very high cells, which are in contact merely by their distal ends. Proximally they are prolonged into delicate processes, by which they are attached to the basement membrane. These cells are of the type of filamentous cells (Hautfadenzellen) described by Eisig ('87, p. 300). Lying nearly in the centre of the cell is the elliptical granular nucleus, which measures 11 by 4 μ. These cells are exactly similar to those contained in the sensory organs before described. Some such cells are seen in Figure 21, *d, f* (Plate II.). In addition to these there are occasional cells in the hypoderm, the nuclei of which are narrower and stain much deeper, which possess a denser, more highly refractive cell body. Figure 21, *a*, *c*, *e*, represents these cells, which are seen *in situ* at *cl. sns.*, Figure 23. These may be sensory cells; I was, however, unable to discover the sensory hairs described by Selenka ('83, p. xvii) as found on the external surface; these cells certainly possessed merely such cilia as those adjacent. At the level of the mouth there is a transition from these filamentous cells to the columnar cells of the intestinal tract. This serves to fix the level of the oral opening proper, which would otherwise be indefinite on account of the various degrees of expansion or contraction of the animal.

b. Migratory Corpuscles.

Between these filamentous cells are found at varying heights highly refractive spherical nuclei 4 μ in diameter. My attention was first called to them in a preparation stained by Hamann's carmine (Plate II. Fig. 15), where they become prominent by reason of their being stained deeper than the other nuclei. A more careful examination showed that they were not accidental, as at first surmised, but definite independent structures. Each is surrounded by an irregular clear zone varying in width from a mere line to one half the diameter of the nucleus. By means of these peculiarities, such cells were traced back through the cutis, where they were most abundant in the spaces just below the basement membrane, to the blood cavity, and were found to agree precisely in size and optical character with one kind of blood corpuscle found in the coagulum there. They may then be regarded as migratory corpuscles or leucocytes, analogous perhaps to those of vertebrates. Similar cells are often met with, though never in such numbers, throughout the body wall.

The thin basement membrane to which the processes of the filamentous cells are attached is not everywhere equally distinct. Owing to the contraction of the different areas, it may be thrown into extensive and complicated folds, which, combined with the basal processes of the filamentous cells, render its identification a matter of difficulty, but in suitable regions it may be identified beyond a doubt.

Beneath this membrane lies a cutis, very similar to that of the body wall. It differs chiefly in the scarcity of pigment cells and in the entire absence of glands. The "Wimperdrüsen" seen by Vogt und Yung ('88, p. 406) on the oral surface of the tentacles, are merely appearances due to unequal contraction of certain areas, which produces structures superficially similar to the sensory organs of the anterior papillate zone already described. The cutis is further peculiar in the possession of numerous muscular elements, which are primarily arranged about the blood cavity. The relation of these to the body musculature is of considerable interest.

c. *Musculature.*

If a transverse section be made in the plane of the annular mass of muscle surrounding the pharynx which is produced by the fusion of the four retractors, there appears only an indefinite mass of confused fibres. If, however, the section be cut in any longitudinal plane, it will be seen that the longitudinal fibres which compose this mass divide into two unequal parts, each of which draws its fibres from all parts of the original muscular mass. In such sections each of these portions appears like a band; the smaller curves over into the muscularis of the body wall of the introvert, or rather goes to form the longitudinal muscles of this, its fibres being directly continuous with those of the predominant longitudinal layer. The other and larger portion ascends into the tentacular fold; a few of its fibres follow the aboral surface of the blood cavity, but by far the greater number are continuous as an apparent muscular band along the oral side of the cavity immediately adjacent to the latter. At the base of the tentacular fold it is thickest, measuring half the thickness of the oral wall in which it lies; but as it advances distad through the tentacular fold, fibres are continually given off peripherally, so that they radiate toward the surface. These terminate in the vacuolated portion of the cutis in some manner not exactly determined. In this way the muscular band becomes looser and looser by the gradual loss of its elements, until at the tip of the tentacle only a few fibres remain, which attach themselves there. In cross sections the tentacular fold shows a few circular fibres, immediately adjacent to the blood cavity, which turn into the trabeculæ and cross into the corresponding layer of the opposite wall of the fold. In addition to these, the trabeculæ have other fibres which cut the muscular band at right angles, and run from one side of the tentacular fold to the other. At the outside of the muscular band there can be found usually a few circular fibres. If one considers that this muscular band, prominent in longitudinal sections through any plane, thus represents a muscular sheet extending throughout the whole tentacular fold, and that this lies in the cutis of the oral, or in an expanded condition *convex*, surface of the blood cavity, with its fibres radiating into every fold of the tentacles, — if one remembers, further, that it is at its base connected with the fused retractors, and is in fact merely an extension of them, — then its action in the inversion of the tentacles by drawing in and packing together the various folds and plaits becomes at once clear. Furthermore, the muscles concerned in emptying the blood cavity are primarily the powerful trabeculæ and the longitudinal muscles, whereas the circular muscles, which are comparatively scanty, are only of secondary importance.

The cutis of the oral fold contains also numerous vacuoles in groups near the basement membrane, and these may be seen in transverse sections filled with the migratory cells previously mentioned. In addition to these small leucocytes, occasional larger granular cells are found in the lacunæ. These correspond again to the granular corpuscles of the blood. They do not make their way into the hypodermis. A tissue which might be homologized with the supporting tissue of Phoronis does not, according to my observations, exist in this form.[1]

Lastly, lining the blood cavity and covering the trabeculæ is an endothelium of very flat cells with proportionally large nuclei. This endothelial lining is continuous, and is adjacent to a mass of gelatinous connective tissue, which is without vacuoles, so that the blood corpuscles could reach the hypodermis only by a definite migration through the endothelium and the connective tissue. The cavity is often distended by a coagulum which contains corpuscles that, as various writers have maintained, actually differ in size from those of the cœlomic fluid, so that a connection between the two cavities was regarded as improbable. I can confirm the statement of previous writers that no such connection exists. Yet as the corpuscles are in size between the extremes of those in the cœlomic fluid, and not far from the average (*cf.* the exact measurements of Brandt, '70, p. 3), it is not improbable, in view of the migratory tendency of the corpuscles already described, that the cœlomic fluid receives its quantum from the blood system by the active emigration of the corpuscles which are formed in that system. This was conjectured by Brandt ('70, p. 24), who had found, however, no evidence of such a tendency on the part of the corpuscles. The detailed and careful account of the vascular system given by him has been overlooked by many later investigators.

d. Vascular System.

In contradistinction to Sipunculus Gouldii and to Phascolosoma, the blood cavities of S. nudus are not in the form of regular vessels, but are indefinite lacunar spaces, traversed by trabeculæ at irregular intervals and extending throughout the whole tentacular fold, everywhere almost equally distant from the exterior.

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[1] See Addendum.

Numerous facts have been adduced by Andrews ('90, p. 419) to prove the branchial nature of the tentacles in S. Gouldii, chiefly the circulation and the red coloring matter of the corpuscles. Certain structural and other peculiarities compel me to deny the respiratory nature of this system in S. nudus. As was pointed out by Brandt ('70, p. 23), the extreme thickness of the layer of connective tissue in the tentacles would militate against the opinion that respiration takes place to any considerable extent in this part. Furthermore, although I have watched S. nudus in aquaria for considerable periods of time, not only when they were lying upon glass, but also when they were on the surface of the sand, and in their burrows wherever these were adjacent to the glass so as to permit observation, I have seen the tentacles extruded but seldom, and never for more than a second or two, until the water had become so impure as to partially narcotize the animals. The respiratory value of the tentacles when retracted cannot be regarded as very important!

But the greatest objection to assigning a respiratory character to this system would seem to be the utter inadequacy of the internal mediation between the vessels and the cœlomic fluid. The possible importance of this system in a respiratory direction must be seriously questioned when one considers that the ring canal and the two blind sacs (in S. Gouldii but one!) buried in the connective tissue of the œsophagus, which at best expose but one half their surface to the cœlomic liquid, are the only means of transmitting oxygen from the so-called vascular system to the general body fluid. The observations of Keferstein ('62, p. 47) upon living animals — these were made on Phascolosoma elongatum of a few millimeters in length and fully transparent — showed a constant movement of the fluid, but no passage of it from the vessels into the tentacles, or *vice versa*, except under considerable pressure or violent injuries.

The probable lack of respiratory function in the vascular system cannot be extended to all Sipunculids. In this connection it is of great interest to notice that various species are provided (Selenka, '83, p. xix) with several or many branched lateral appendages attached to the blind sac. Such organs are found in Phascolosoma Semperi, P. maniceps, Phymosoma asser, Dendrostoma signifer, *et al.* All of these forms possess, according to the same author, long thin filamentous tentacles (*cf.* his generic descriptions and figures). This peculiarity suggests at once the probability of a respiratory nature for the tentacles; and its occurrence in single species of various genera would indicate that it is a secondarily acquired function.[1]

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[1] See Addendum.

The numerous dermal canals close under the hypodermis of S. nudus are unquestionably of great value in respiration, and the region of the introvert, which is distinguished by thin cuticular and muscular layers, actually not so thick as the walls of the tentacular fold, presents a far greater surface for the transmission of oxygen directly to the cœlomic fluid than the entire vascular system.

Primarily, then, this system is hydrostatic, and this is probably its chief function in S. nudus. The dorsal and ventral vessels are reservoirs into which the fluid is driven by the contraction of the tentacular fold. On the other hand, the muscular walls of these vessels serve to force the fluid out into the lacunæ of the tentacular fold, and thus to move and expand the latter. The varying contraction of these two sets of muscular elements gives rise to the constantly changing form of the tentacles, as the fluid is driven to and fro. This movement might easily simulate, or even under certain conditions become, a circulation. Moreover, any method of killing which worked violent contraction would distort the tentacular fold by driving the fluid into the extreme distal ends of the lacunæ, or by drawing together the entire mass of the tentacular fold, and forcing the fluid back into the dorsal or ventral vessel. It is probably in this way that the lobed or cut form was produced, which has been given as the typical one in all generic descriptions hitherto published. It is worthy of notice that those animals which were killed with expanded tentacles showed the walls of both dorsal and ventral vessels almost in contact, whereas in those which had retracted their tentacles these vessels were so filled by masses of coagulum as to reach a considerable diameter. The probable function, then, of the dorsal and ventral vessels is to receive and hold the fluid forced out of the tentacles at the time of inversion of the introvert.

e. Aboral Wall.

The aboral wall of the tentacular fold differs from the oral chiefly in the undifferentiated condition of the hypoderm. The latter is here composed of low non-ciliated cells, identical with the hypodermis of the general body wall, except where it is elevated into the papillæ or sensory organs already described. Sensory cells are wanting. The cutis of the aboral wall lacks the vacuoles which characterize that of the oral wall, and there are only very few leucocytes to be found.

The thin cuticula, cilia, and sensory cells of the oral, as well as the general sense organs of the aboral, wall of the tentacular fold, show it to be a most important organ of touch. This view is strengthened by the large nervous supply it receives from the brain direct. The cilia undoubtedly aid in propulsion of food particles into the mouth.

3. Nervous System.

a. Brain.

The supraœsophageal ganglion (*gn. su'œ.*, Fig. 3) lies dorsal to the blood sinus, between the two dorsal retractors, and is enveloped by an investment of connective tissue. The posterior surface (Plate II. Fig. 22) is marked by a considerable incision in the median plane, and the anterior dorsal margin bears numerous digitate processes, which project into the cœlomic liquid. In sagittal sections the brain appears nearly flat on its ventral side, whereas the dorsal aspect is considerably curved. As seen from transverse sections, however, the dorsal surface is plane, while a deep median furrow (Plate III. Fig. 25) penetrates the ventral wall. Posteriorly (Fig. 25) this is continuous with a partition which divides the brain into two symmetrical lobes. Anteriorly (Fig. 24) the partition fails, and the division is only indicated by the furrow. On the antero-ventral surface is the termination of the cerebral canal (*cf. infra*).

The entire ganglion is covered by a capsule (Fig. 25, *cps. enc.*), the origin of which can only be determined by the consideration of a series of transverse sections. Following such a series from a short distance posterior to the brain, it will be seen that the septum joining the two dorsal retractors is here fused with the dorsal wall of the œsophagus, in which lies the dorsal vessel. As the posterior extremity of the brain is reached, this septum rises upon the brain, covering its dorsal aspect, and still showing laterally the connection with the dorsal retractors. Immediately inferior to the brain lies the dorsal vessel (Fig. 25, *va. sng. d.*), or, anterior to this, the blood sinus, which is separated from the brain only by its own wall, which thus forms the ventral covering of the brain. The dorsal and ventral layers of the capsule are continuous on those parts of the lateral aspect of the brain where there are no outgoing nerve stems; but when the latter exist, a neighboring portion of the brain capsule is reflected over them to form the neurilemma (Fig. 25, *con't. tis.*). This composite capsule is made up of a loosely woven mass of fibres which often show a plaited arrangement. The discoid nuclei measure 3.5 by 5 μ, and are deeply stained in all coloring fluids. Inferior to this basketwork of fibres are found occasional nuclei, which stain very faintly and possess each a few small nucleoli. These are surrounded by a small amount of a granular substance, and are very similar to nuclei found in the midst of the meshes of the brain itself. Passing inward from this external capsule and directly continuous with its elements, fibres penetrate the brain in every direction, either in definite strands, or in a delicate network surrounding the ganglionic cells (Fig. 25). The fibres which make up these meshes are finer than most of those composing the capsule itself, and recall strongly the finer elements of the cutis. With these they also agree in the possession of minute elongated nuclei, although the clear nuclei previously mentioned are by no means rare. These fibres surround each ganglionic cell with a definite covering (Plate III. Fig. 32) of interlacing elements from which others pass off tangentially to neighboring cells. (*Cf.* Rohde, '87, Taf. IV. Fig. 44–68.)

Ganglionic Cells. — None of the many previous writers on Sipunculus have considered the histological elements of the central nervous system more than cursorily, so that a more extended description of these may be of interest, especially for comparison with the recent exact determination of these elements in many other groups of worms. All the ganglionic cells which were so situated as to admit of a positive answer to the question of their polarity were unipolar, though by no means always unifilar. Such cells as were accurately determined were usually peripheral, since the mass of other fibres and the confusion of many cells make an accurate determination in the case of those cells which are located in the centre of the nervous mass often impossible. I am inclined to think that in the latter region there are multipolar cells, although the demonstration of these was not wholly satisfactory. The cells are uniformly without any proper cell membrane. Each lies enveloped in a covering of delicate connective-tissue fibres (Plate III. Fig. 32), which accompanies the fibrous processes in the form of a delicate sheath (neuroglia). These enveloping fibres are a part of the meshwork which has already been described as arising from its external capsule, and penetrating through the whole brain.

Of all the ganglionic cells, the smallest (Plate III. Figs. 24, 25, *cl. gn. I.*), which usually appear simply as nuclei measuring 6 by 4 μ (Fig. 30), are the most abundant. They are highly refractive, and show a great affinity for coloring matter. There is a nuclear membrane which is stained deeply, as are also the numerous (4 to 10) nucleoli; between the latter many minute chromatine granules are distinguishable with a high power. These nuclei seem somewhat irregular in shape, varying from circular to oval. This variation I regard as due to the direction of the plane of section, and consider the true form as oval. In most cases it is impossible to find even a trace of a cell body, and I was at first inclined to doubt the presence of any recognizable cell substance, and consequently to compare them with the "Nervenkerne" described by Rohde ('87, p. 30). But at length fortunate staining and thin sectioning showed unmistakably the presence, in many cases at least, of an extremely small cell body, such as is shown together with the nerve fibre in Figure 31. It will be noticed that the nucleus is oval in this case, and that the nerve fibre proceeds from one of the small ends of the oval. This fact, as well as the variation in form noticed by careful focusing on the nuclei, would seem to warrant the assumption that these nuclei are uniformly oval. From the diminutive size and transparency of the cell body in comparison with the highly refractive nucleus, it is at once evident that the former can be seen only under the most favorable circumstances. Since I was unable to find any difference in position, size, or optical qualities between these and the other nuclei of similar size and appearance, I feel justified in maintaining the existence of such a cell body for all nuclei of the class.

The second sort of ganglionic cell (*cl. gn. II.*) is distinguished by the presence of a much larger cell body (Plate III. Fig. 29). The nuclei correspond so exactly to those of the first class that they can hardly be distinguished from them. I was unable to see that they were either more or less deeply stained, or that they were, on the average, larger or smaller than nuclei of the first sort. The great difference is in the cell bodies, which in this case are several times larger than the nucleus, measuring 20 by 14 μ, and always evident on account of their slight affinity for stains. One or more vacuoles of non-colored matter, the paramitome of recent writers, may always be found, and in favorable cases there can be seen such a distribution of these as is shown in Figure 32. The *paramitome* exists in the form of numerous peripheral vacuoles subjacent to the enveloping connective fibres, and possibly (?) surrounded by them. The nucleus lies in a zone of clear matter, while the *mitome*, or filar substance, appears densest external to this. Between these and the first sort of ganglionic elements there exists every possible transition, so that this class is but poorly marked off from the preceding one. The vast majority of these cells are, however, of approximately uniform size, and I therefore cannot agree with Nansen ('87, *note*, pp. 113, 114) when he maintains that such transitional forms forbid the grouping of these cells in different classes. Such intermediate forms serve rather to explain the development of the one type from the other, without detracting from the individuality of either class.

The third type is that of the large[1] cells, represented in Figure 28, Plate III. These vary considerably in size and shape; the mean longitudinal diameter is 55 μ, the transverse 40 μ. The cell protoplasm stains rather deeply, and is notably granular. These granules resolve themselves in the nerve processes into fine lines. Each large ganglionic cell contains a number of clear spaces, the paramitome, exactly similar to those already described for cells of the second class; and these are often arranged concentrically, and more or less regularly along the periphery of the cell. The single nucleus, 15 by 12 μ in diameter, is usually found nearer the end of the cell from which the nerve fibre emerges, and, in contrast with those already described, is stained only lightly. A nuclear membrane is very distinct, and there is one large nucleolus 2–3 μ in diameter. In rare cases two smaller nucleoli were found, never more. The nucleus also contains numerous fine granules of chromatine, which are very distinct in the matrix, which remains completely unstained. Nuclei of this class are not infrequently crescentic, with a clear space enclosed by the horns of the crescent, corresponding exactly to such forms as are figured by Rhode ('87, Taf. IV. Fig. 51 *et al.*). Although variable, these cells represent a more isolated type than either of the other classes, and intermediate forms, especially in nuclear appearance and structure, are rarely seen in the brain.

An examination of the ventral nerve cord in transverse section shows a preponderance of cells of the second class. The first class is poorly represented, though the size of the plasmatic portion varies greatly in different cells. Occasionally one finds cells which in their deep staining and nuclear appearance recall the large cells of the brain. But measurements showed one such cell to be only 24 by 30 μ and its nucleus 7 by 11 μ in diameter, dimensions which are far smaller than those of the average of the large cells in the brain. These cells do not seem to be regularly arranged in the ventral nerve cord, and no grouping could be found which suggested metamerism. The peripheral nervous plexi possess very few ganglionic elements, and these few are not reducible to the types present in the central nervous system, for they are invariably multipolar, and are situated at the crossing or branching of fibres.

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[1] It is much better, for the sake of clearness in neurological terminology, to keep the term "giant cells" (Riesenzellen) for the huge elements in the nervous system of Nemertines, Annelids, *et al.*, as German writers have done, than, with Shipley ('90, p. 16) and Andrews ('90, p. 424), to apply the term to such cells as I have placed in the third class, to which the former are at most only remotely homologous.

The *internal structure of the brain* shows a strictly bilateral arrangement of the elements. A transverse section through the middle of the ganglionic mass is represented in Figure 24 (Plate III.). The fibrous matter is collected into two commissural masses, in which the fibres run both anteroposteriad, chiefly at the lateral extremities, and laterally, chiefly in the middle. The real relation of these commissures to each other is first seen in sagittal sections (Plate II. Figs. 19 and 20), where the fibrous matter has the form of a > with the apex directed forward. The dorsal arm of this > is prolonged backwards in two lateral horns, which are surrounded by ganglionic cells. The tips of these horns, cut transversely, are seen in Figure 25 (Plate III.). The similar ventral horns are the roots of the circumœsophageal connectives. From near the anterior apex of the > a small arm of fibrous matter is directed forward, as seen in a sagittal section of the brain near its left lateral margin (Plate II. Fig. 19). This becomes, in a median sagittal section, a small commissure cut transversely (*coms. a.*, Fig. 20), and separated from the brain by the connective-tissue capsule. This commissure is at its right side again connected with the brain, as already described, for the left extremity. Thus it resembles in its form and relation to the main fibrous mass of the brain the handle of a basket, the handle being directed forward. It lies, as can be easily seen from the figures, immediately below the surface of the cerebral organ, and its relation to that structure will be more fully explained later.

The arrangement of the ganglionic elements in the brain is somewhat definite. Ganglionic cells of the first sort are found in nearly every part, and make up all diffuse centres, where, however, transitional forms render their separation from the second class difficult. The former are most strongly marked at the tip of the dorsal horn (*cl. gn. I.*, Fig. 25), where they are very densely crowded. They cover also the lateral and dorso-lateral aspects of the dorsal commissure (Fig. 24) in similar dense masses. The anterior face of the fibrous matter is also almost exclusively occupied by cells of the first class; and from this region they extend a short distance ventrally. Here one finds a gradual transition into the ganglionic cells of the second class (*cl. gn. II.*, Plate II. Fig. 20, Plate III. Fig. 24), which occupy the entire ventral and posterior aspects of the fibrous matter. These cells also fill the space between the dorsal and ventral commissures, but are found dorsally only between the two lateral fibrous swellings on the lateral edges of the dorsal commissure. They are never so crowded as cells of the first class, and display no particular arrangement into clusters or groups.

The large ganglion cells of the third class (*cl. gn. III.*) are present in a somewhat limited number, and always in a definite position. They lie in the posterior third of the brain, on its medial posterior boundary (Figs. 19, 20, 25). The large fibres which pass off from these cells are easily seen to turn toward the opposite side of the body and to make their way into the ventral commissure, where they are lost to view, either because they are split up into a number of small ones, or from some other cause suffer a diminution in diameter. This crossing of fibres from cells on one side of the body to the connective[1] of the other certainly does not take place frequently in either of the other two groups of ganglionic cells. Wherever circumstances permitted the following of nervous processes in groups I. and II., these were seen to pass off towards the connective on the same side of the body as the cell itself.

b. Cerebral Nerves.

From either side of the brain two groups of nerves pass off; the anterior consists simply of the first tentacular nerve (*n. ta. 1,* Fig. 22, Plate II.); the posterior contains the second, third, and fourth tentacular nerves and the œsophageal connective. The tentacular nerves radiate from the brain to the aboral wall of the tentacular fold, and, splitting there into numerous branches, follow the aboral wall of the blood cavity toward the distal margin of the fold. The first tentacular nerve supplies that portion which was designated as the dorsal horn. Following the margin of the fold from this region toward the ventral line, its successive parts are seen to receive their nerve supply from the third, second, and fourth tentacular nerves successively. Each of these innervates about equal portions of the fold. I was unable to trace the ultimate termination of the nerves in this region.

The œsophageal connectives give off each three branches: (1) the splanchnic, (2) the muscular, and (3) the inferior muscular. The splanchnic is given off ventrally and medially immediately after the connective leaves the ganglion (*n. spl.*, Figs. 22, 25). It passes diagonally forward, — *not posteriad,*[2] *as stated by other writers,*[3] — and into the circular muscles of the pharynx, where it terminates in a distinct ring at about the level of the middle of the brain.

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[1] I use the word *connective* in the sense first suggested by Lacaze-Duthiers, to distinguish the nerve fibres joining ganglionic nerve centres which are on the same side of the body, reserving the word *commissure* for such fibres as cross the median plane of the body.

[2] This nerve is turned backward in Figure 22, for the sake of clearness in the drawing. Normally, it extends forward *under* the ganglion.

[3] This relation is obscured when the introvert is slightly retracted, and even apparently reversed when the retraction is greater.

At the point where the splanchnic nerve forms a ring around the pharynx one finds a few nerve cells, but they are few in number, and hardly deserve the name of a ganglion. From this ring it is easy to trace in serial sections the stems of the intestinal plexus, which are here large. This plexus lies in the connective tissue of the intestinal wall, and was first described by Andrews ('90, p. 405) for S. Gouldii. However, he failed to find a splanchnic ring, or any anterior connection of the plexus with the central nervous system.

The muscular branch (*n. mu. rvt.*) passes off laterally from the middle of the œsophageal connective, and divides near the centre of the fused mass of the dorsal and ventral retractors into two branches, one of which traverses each retractor. Not far behind this branch there is upon the connective a small trunk (*, Fig. 22), which passes to the surface of the muscular mass, but which could not be traced farther. It remained doubtful whether this was a subsidiary muscular branch or of other value.

c. *Ventral Nerve Cord and Plexi.*

After the union of the two connectives, the ventral nerve cord thus formed floats a short distance free in the body cavity, and sends off numerous long nerves to the body wall. The first of these, the composite nerve of Andreae ('81, p. 248), is by no means always composed of eight branches in a single sheath, as stated by that author. The number varies from six to nine, and the size of the different trunks varies as well (Plate II. Fig. 22, *I.*). In fact, the later branches, which according to him consist of two trunks, one from each side of the nerve cord, not only show great variability in the size of these trunks (Fig. 22, *II.*), but also at times only a single trunk can be found, which then comes from but one side of the nerve cord. All these frequent irregularities point to a lack of metamerism in the nervous system. On reaching the body wall these nerves branch in a digitate manner through the muscles of the introvert, the main trunks being longitudinal, and do not form nervous rings around the body as in other parts of the wall. From these longitudinal stems large trunks pass outward through the musculature to the dermal plexus.

This dermal plexus lies in the cutis at its plane of union with the musculature, and consists of large longitudinal trunks (*plx. n. drm.*, Plate I. Fig. 4) with lateral anastomoses. From this network, fibres (*rm. gl.*)

pass outward through the cutis to the multicellular glands and to the hypodermal cells, as already described, as well as inward (*rm. mu.*) to the muscles. The existence of such a plexus has already been shown by Andrews ('90, p. 395) for S. Gouldii. To his description, which answers equally well for S. nudus, I can only add a few observations as to the histology of the nerve trunks. Each of these possesses a well defined sheath or neuroglia (*n'gl.*, Fig. 5), in which discoid nuclei (*n'gl. nl.*) measuring 2 by 4.5 by 6 μ are common. These nuclei lie either inside or outside of the membrane; they may be stained deeply, and contain many nucleoli. The substance inside the neuroglia has a distinct fibrillar appearance, and when these nerve stems were bent upon themselves so as to be cut transversely and still extend longitudinally within the same section, the fibrillæ appear in the transverse section as dots. These are also the fibres which are connected with the cells of the multicellular glands (*gl.''' n. fbr.*, Plate I. Fig. 14).

The existence of the peritoneal plexus found by Andrews ('90, p. 395) in S. Gouldii could not be demonstrated in preserved specimens. No doubt the examination of fresh material will show its presence in S. nudus as well.

4. Cerebral Organ.

This interesting structure may be considered under two heads: first, the canal; and secondly, the surface next to the brain, or the cerebral organ proper.

The canal opens, as already described, on the dorsal median line, just posterior to the tentacular fold (*can. o. ceb.*, Figs. 2 and 3). From this point it extends posteriad about 1.5 to 2 mm., to the anterior ventral surface of the brain, where it terminates blindly (*o. ceb.*, Fig. 3). From the marginal fold which surrounds the opening arise numerous longitudinal ridges, which traverse the entire canal, and give it in transverse section (*can. o. ceb.*, Plate III. Fig. 26) a branched appearance. In a surface view the walls of the canal appear thickly spotted with brown, and further examination shows this to be due to the presence of large numbers of the characteristic pigment cells, which are usually seen crowded in masses along the summits of the ridges (*cl. pig.*, Fig. 26). It is probably this canal which was found by Keferstein und Ehlers ('61, p. 47) in S. tesselatus. The canal is correctly figured (Taf. VII. Fig. 1, 2, *u*, *u'*), but they evidently mistook its true character, since they say: "Ausserdem sieht man vom Hirn zum Tentakelkranz *einen aus zwei Hälften bestehenden, dicken Strang* verlaufen, der dort endet, und an dem Endpunkte, wie man bei der Betrachtung von aussen her wahrnimmt, in der Haut von einer Gruppe kleiner Falten umgeben ist als wenn er *eine Röhre wäre* und hier nach aussen mündete."[1] Among recent writers, Vogt und Yung ('88, p. 404) mention and figure the "cerebral canal," without a more particular description of its structure or morphological relations.[2]

The histological study of the canal shows some features of interest. Its entire surface is lined by an extremely thin cuticula, which appears under high powers merely as a double contour, pierced by numerous short cilia. The cells of the ventral wall of the canal have the appearance of ordinary hypodermal cells, except that they bear cilia. The dorsal wall is made up of similar cells near the mouth of the canal, but these become higher as the brain is neared, until at the middle of the canal they have assumed the form of a high columnar epithelium with large nuclei. This condition is preserved up to the surface of the brain. When examined more closely, these cells are seen to be filled with granules of a highly refractive nature, especially at their distal ends, and may be regarded as the source of the more or less extensive coagulum always found at the basal end of the canal. We have here, then, the secretive portion of this organ.

In cross sections of the canal (Plate III. Fig. 26) one sees clearly a group of muscular fibres which is deflected from the circular layer of the body wall and encircles the canal in the form of a sphincter (*spht.*), which, although most marked at the opening of the canal, is present along its entire extent. The function is evidently to prohibit the entrance of extraneous matter during the forward motion of the animal, and to assist in changing the water contained in the canal. In the latter function it would be assisted by the cilia lining the canal.

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[1] The Italics are not in the original.

[2] P. S. — Since writing the above, I have obtained access to a preliminary communication by Spengel ('77), and find that in this he has maintained "die Existenz eines vom Gehirn zur Basis der Tentakeln führenden, offenen Canales." Spengel was thus the first to arrive at the true form of this structure, but I cannot find that he has anywhere given a more detailed account of its morphological or physiological character. In the same paper he says: "Das Gehirn stellt sich als eine knopfartige Verdickung des diesen Canal auskleidenden, mit der Epidermis zusammenhängenden Epitheles dar." Against this interpretation it may be said that the embryological evidence of Hatschek ('83) makes it probable that the canal is secondarily formed. Furthermore, a histological examination of the parts shows that the brain is less closely connected with the cerebral organ than appears superficially, since the brain capsule separates the two completely, except at the entrance of the anterior commissure, which furnishes the nervous supply to the organ in question. A full discussion of these relations follows the histological description of the cerebral organ which is given later.

At its posterior end the canal widens abruptly into a saucer-shaped cavity, which lies with its concave surface upon the antero-ventral face of the brain (Figs. 3, 20, 27), and includes a low rounded prominence (*o. ceb.*) which I regard as the cerebral organ proper. Macroscopically, this appears to be continuous with the brain, but internally the connective-tissue capsule separates it almost entirely from the ganglionic mass. The histological character of this prominence, and its relation to the brain, require more extended consideration.

When one examines a longitudinal section of this region (Plate III. Fig. 27), perhaps the most striking feature is the extremely prominent cuticula ($4\ \mu$ in thickness), which covers exactly the convex surface, and only that portion, for at the margin of this convexity (†, Fig. 27) it passes abruptly over into the very thin cuticula of the canal wall. At each *lateral* edge of the cavity there is a considerable thickening of the cuticula, which extends a short distance into the subjacent tissue and has in cross section the outline of a small retort. The cuticula presents a sharp outer boundary, and there one finds no remnants of cilia in the sections, yet I am inclined to think that cilia are present in the living animal. For in preserved specimens the entire lower portion of this canal is filled with a granular coagulum, which might easily enclose and obliterate cilia, if indeed any were preserved in this deep and narrow canal, where fluids evidently could not readily penetrate. The lateral cilia, which are perfectly distinct in the anterior half of the canal, become gradually less so, until in the lower portion, which is filled with this coagulum, they entirely disappear. In partly macerated specimens this thick cuticula breaks up into small blocks along lines extending perpendicularly to the surface, so that one may reasonably assume that there is a ciliated condition of this surface in the living animal.

It is difficult to study the cells which underlie this cuticula, inasmuch as the cell boundaries are very indistinct; the most evident feature is the regular row of nuclei which lies close under the cuticula. From these a crowded mass of nuclei (*cl. gn.*?) and fibres extend at right angles to the surface into an irregular group of fibres (transsected in Fig. 27, *coms. a.*), — the anterior commissure already described. If one examines the nuclei, their resemblance in size, shape, and optical properties to those of the central nervous system is evident. An actual entrance of the fibres into this anterior commissure can also be easily observed. The connection of these fibres and nuclei with the hypodermal cells is very difficult to prove in sections; but in a badly preserved and hence partially macerated preparation there was in many places a definite continuity of these cells with the fibres and underlying nuclei. The probability of a direct continuity of the hypodermal cells with the central nervous system through the anterior commissure seems to me to be strong evidence in favor of the special sensory nature of the organ. An examination of its morphological relations also yields much that is favorable to this view.

The existence of a glandular area, the direct connection of the organ with the central nervous system, and its median position near the anterior extremity of the body, all point to its close relationship to such sense organs as are cited by Dewoletzky ('87, p. 278), and as are common in the class Vermes. These have their origin, according to Dewoletzky, in "ein Paar flimmernder Hauteinstülpungen." Whether the same holds for this cerebral organ of Sipunculus can naturally be decided only upon embryological evidence. Hatschek ('83, p. 115) says that toward the close of the larval stage two "Wimpergruben" are formed, one on either side of and near the median line. Further, he says, "Es sind dies wohl Sinnesorgane die sich wahrscheinlich auch am erwachsenen Thiere werden nachweisen lassen." These would by their fusion produce an organ which, in position at least, would correspond to that which I have described; and from the absence of any other structure to which these Wimpergruben can be traced, it is allowable to assume their genetic connection with this cerebral organ until the development shall furnish positive evidence on the question. That this organ might be the apical area (Scheitelfeld) which, by the recession of the brain from the surface, had come to be connected with the exterior by means of a canal, is disproved by Hatschek's ('83, p. 108) observation that there is a complete separation of the ganglion from the body wall at the time of its retreat; according to the same author, the formation of the Wimpergruben was subsequent to this separation.

If, now, the other members of the group of Sipunculids be examined for similar structures, two cases are found which require consideration. Shipley ('90, p. 18) has described an infolding of the preoral lobe which extends to the surface of the brain, and from which a pair of retort-shaped tubes penetrate into the ganglionic mass, one at each dorsal lateral angle of the brain. The cells of the inner limb of the tubes secrete a black pigment. Andrews ('90, p. 418) finds in S. Gouldii two similar tubes proceeding from the lateral edges of a transverse pit anterior to the ridges of the ciliated cushion. These tubes extend into the ganglionic mass, and contain a coagulum, but have no pigment. Comparing these two accounts with each other and with that just given of the cerebral organ in S. nudus, it will be seen that the tubes lack pigment in S. Gouldii, and that both tubes and pigment are wanting in S. nudus, unless the regions of thickening in the cuticula on the lateral aspect of the cerebral organ noted above be the rudiments of such structures. The optic nature claimed by Shipley for the tubes in Phymosoma agrees with their reduction or disappearance in the forms inhabiting the sand. The position of the organs would seem to indicate an homology between the ciliated cushion of S. Gouldii, the deep pit of the preoral lobe in Phymosoma, and the cerebral organ in S. nudus. As to the histological character of the organ in Phymosoma, nothing is found in the account of Shipley. Andrews describes that of S. Gouldii as ciliated and well supplied with nerves. The deep location of the organ in S. nudus may be merely for protection, or perhaps due to the development of the glandular area, or even necessitated by the recession of the brain from the surface. The canal is much longer in S. tesselatus, where the brain also lies deeper in the body, than in S. nudus. An analogous variation may be seen in the deep-seated lateral organs of the Enopla as compared with those of the Anopla.

Finally, if it be asked why the whole structure may not be regarded as a degenerate organ, of which the pigmented tubes were originally the active portion, I can only say that the active glandular area and ciliated canal cannot be explained on such an assumption, and still less can the special nervous supply. I studied the structure a long time with this idea in mind, but finally became convinced that it was untenable in every respect. Although the evidence is far from complete, I regard it as an actively functional organ, morphologically the equivalent of the ciliated cushion of Phascolosomes, and possibly with a more highly specialized function, since it certainly has a more highly differentiated form.

Such organs are by no means rare. Dewoletzky ('87, p. 277) has given a list of similar ones, and has considered at length their probable function, which he regards as "some sort of general perception as to the character of the surrounding medium."

IV. Conclusions.

If now the account I have given of certain points in the anatomy and histology of S. nudus be compared with that given by Andrews ('90) for S. Gouldii, it will be noticed that, while there is a general similarity, a correspondence in details is wanting. The dermal glands are hardly more than similar in type, and a direct correspondence between the different kinds is not to be found ; for the bicellular are entirely wanting in S. Gouldii, and the multicellular of S. nudus agree with neither group described for S. Gouldii. Whether the non-glandular organs of Andrews correspond to the small papillæ described above cannot be definitely determined, on account of the brevity of Andrews's description and the lack of figures. On the other hand, Andrews has emphasized the fact that a close agreement exists between the dermal bodies of S. Gouldii and those of various Phascolosomes. Again, in the arrangement of the musculature, in the uniform unbanded circular layer, in the absence of diagonal fibres, and in numerous other details, S. Gouldii is unlike S. nudus, and in the same degree that the former resembles Phascolosoma. In the light of these facts, a modification of the generic characters given by Selenka ('83) to Sipunculus, which include S. Gouldii in the same genus with S. nudus, would seem advisable.

Striking as is the similarity between the anatomy of the nervous system in the Annelids and in the Sipunculids, certain characteristic differences are worthy of note. The peripheral system of plexuses is very highly developed in the latter, and consists almost entirely of fibres, whereas the dermal plexus of Capitellids, Nemertines, and Polychæts is composed largely of ganglionic cells. In the ventral nerve cord of Sipunculids there is no metameric arrangement of the lateral branches, nor any concentrations of the ganglionic elements in the cord itself. On the other hand, there is present a splanchnic nerve and an intestinal plexus in both Sipunculids and Annulata, and the complicated structure of the supraœsophageal ganglion in Sipunculus agrees in general with that of various Annelids and Nemertines.

As regards the histology of the central nervous system, it will be noticed that the description given in this paper for S. nudus corresponds closely with that given by Rohde ('87) for Chætopods, and by Bürger ('90) for Nemertines. It is of interest, however, to note more exactly the points of likeness and difference. If further investigation should lead to the discovery of a minimal cell body for the nervous nuclei (Nervenkerne) of Rohde, — and I think this probable on account of the extreme difficulty experienced by Bürger ('90, p. 106) and myself in finding this cell substance, — then these nervous nuclei would correspond in general character and occurrence with the first class of ganglionic cells described by Bürger in Nemertines, and with the first type in Sipunculus. The first class of Rohde agrees in general with the second of Bürger ; but both differ from the second type in Sipunculus in one important point, namely, their arrangement. While they are (always?) found grouped in clusters in the brains of Polychæts and Nemertines, such an arrangement is never unquestionably present in Sipunculus, though indications of a regular grouping were sometimes noticed. This may be regarded, perhaps, as indicating a less highly specialized condition in the Sipunculid nervous system. According to Rohde and Bürger, these cells have nuclei slightly smaller and more deeply stained than those of the first class. I did not find any such difference between the two groups in Sipunculus. The third type of cells in the Sipunculid brain shows also a general correspondence to Class III. of the Nemertines and Class II. of the Chætopods. In both Chætopods and Nemertines there exists a fourth type, — the paired "giant cells" of the central nervous system, with their accompanying "giant fibres." These are entirely lacking in the Sipunculids. No one of the large cells has acquired any uniform or considerable superiority of size over its fellows. Furthermore, no giant fibres can be found in the ventral nerve cord, so that these elements probably do not exist in the Sipunculid nervous system. This may be regarded as further proof of the lower grade of specialization in the Sipunculids.

The earlier investigators regarded these "giant cells" as "Bildungen ganz verschiedener Art" (Spengel, '81, p. 40), but the more recent writers incline toward the opinion that they are homologous throughout (Eisig, '87, and Friedländer, '89). Now, either these "giant cells" are neomorphic in both groups, and hence not at all homologous, or the Sipunculids were separated from the primitive stem before the separation of Nemertines and Annelids took place, and before the differentiation of these elements had been effected. A complete disappearance of giant cells and giant fibres in the Sipunculids is hardly probable, in the light of the persistence of these and all other nervous structures. This would put the origin of the Sipunculids farther back than has usually been maintained, and would make their relationship to the Annelids somewhat distant. Of importance in this connection is the simple undifferentiated condition of the ventral nerve cord, which shows no trace of a metameric concentration of ganglionic cells, such as is found in the Annelids. According to the researches of Andrews ('90), moreover, the lateral branches lack that metameric character which has heretofore been assigned to them, and I have been able to confirm this in part for S. nudus. Lack of metamerism in the adult, as well as in the larva, would serve to strengthen the view of only a remote relationship between Annelids and Sipunculids, as has long been maintained by Hatschek ('80 and '83) on embryological grounds.

The existence of at least giant fibres has been proved for Echiurus by the researches of Greeff ('79) and Spengel ('80, p. 487), and more recently for Thalassema by Rietsch ('86, p. 402), so that the presence of corresponding ganglionic cells may be reasonably assumed. This is, then, a further ground for separating the Sipunculids from the Echiurids, and for assigning to the latter a closer relationship to the Annelids than the former have. This position has been defended from an embryological standpoint by Hatschek ('80, p. 71) and Conn ('86, p. 399).

In spite of the well known conservatism of the nervous system, I am well aware of the dangers of such conclusions based upon the study of a single system or a single form. The foregoing comparison is offered, then, merely as a new side light on the unsettled question of the position of the Sipunculids, and in the hope that the accumulation of evidence from various sources may some day bring a clear and full solution of the problem.

January 20, 1891.

Addendum.

During the correction of the proof-sheets there has appeared a second paper by Shipley ('91) on Phymosoma (P. Weldonii, *n. s.*). It is interesting to note that the gland cells there described (p. 114) correspond very closely to the multicellular glands of S. nudus, except that no connection with nerve fibres is reported. Shipley affirms positively (p. 115) "the absence of those skeletal cells which formed so interesting a feature" of P. varians (Shipley, '90, p. 9). That such a tissue does not exist in S. nudus has already been emphasized. This is then strong proof that it is an individual peculiarity of the one species, rather than an ancestral relic. In general the claimed relationship of Sipunculids and Phoronis seems to me to have little in its favor beyond the external similarity of the two forms.

It is a pleasure to see that Shipley and I have both arrived independently at the same conclusions regarding the vascular system. He ('91, p. 116) does not regard it as important in respiration, and explains the cæcal diverticula of the dorsal vessel, which might be looked upon as strengthening the view of its respiratory nature, as merely reservoirs for the increased overflow from the tentacles, which are exceptionally numerous in this species.

BIBLIOGRAPHY.

Ambronn, H.

'90. Cellulose-Reaction bei Arthropoden und Mollusken. Mitth. aus d. Zool. Station Neapel, Bd. IX. Heft 3, pp. 475–478. 15. Juni, 1890.

Andreae, J.

'81. Beiträge zur Anatomie und Histologie des Sipunculus nudus, L. Zeitschr. f. wiss. Zool., Bd. XXXVI. Heft 2, pp. 201–258, Taf. XII., XIII. 1. Nov., 1881.

Andrews, E. A.

'90. Notes on the Anatomy of Sipunculus Gouldii, Pourtalès. Studies Biol. Lab. Johns Hopkins Univ., Vol. IV. No. 7, pp. 389–430, Pl. XLIV.–XLVII. Oct., 1890.

Brandt, A.

'70. Anatomisch-histologische Untersuchungen über den Sipunculus nudus, L. Mém. de l'Acad. Imp. d. Sci. d. St. Pétersbourg, VII^{e} Sér. Tom. XVI. No. 8, pp. 1–46, Taf. I., II. 10 Fév., 1870.

Bürger, O.

'90. Untersuchungen über die Anatomie und Histologie der Nemertinen nebst Beiträgen zur Systematik. Zeitschr. f. wiss. Zool., Bd. L. Hefte 1, 2, pp. 1–277, Taf. I.–X. 10. Juni, 1890.

Conn, H. W.

'86. Life History of Thalassema. Studies Biol. Lab. Johns Hopkins Univ., Vol. III. No. 7, pp. 351–401, Pl. XX.–XXIII. June, 1886.

Dewoletzky, R.

'87. Das Seitenorgan der Nemertinen. Arb. aus d. zool. Inst. Wien, Tom. VII. Heft 2, pp. 233–280, Taf. XII., XIII.

Eisig, H.

'87. Monographie der Capitelliden des Golfes von Neapel. Fauna u. Flora d. Golfes v. Neapel, No. XVI. xxvi + 905 pp., 37 Taf.

Friedländer, B.

'89. Ueber die markhaltigen Nervenfasern und Neurochorde der Crustaceen und Anneliden. Mitth. aus d. Zool. Station Neapel, Bd. IX. Heft 2, pp. 205–265, Taf. VIII. 24. Sept., 1889.

Greeff, R.

'79. Die Echiuren (Gephyrea armata). Nova Acta k. Leop.-Car. deutsch. Acad. d. Naturforscher, Bd. XLI. Pt. 2, No. 1, pp. 1–172, Taf. XVI.–XXIV.

Hatschek, B.

'80. Ueber Entwickelungsgeschichte von Echiurus und die systematische Stellung der Echiuridæ. Arb. aus d. zool. Inst. Wien, Tom. III. Heft 1, pp. 45–78, Taf. IV.–VI.

'83. Ueber Entwickelung von Sipunculus nudus. Arb. aus d. zool. Inst. Wien, Tom. V. Heft 1, pp. 61–140, Taf. IV.–IX.

Hoyer, H.

'90. Ueber den Nachweis des Mucins in Geweben mittelst der Färbemethode. Arch. f. mik. Anat., Bd. XXXVI. Heft 2, pp. 310–374. 27. Sept., 1890.

Keferstein, W.

'62. Untersuchungen über niedere Seethiere. Zeitschr. f. wiss. Zool., Bd. XII. Heft 1, pp. 1–148, Taf. I.–XI. 16. Juni, 1862.

'65. Beiträge zur anatomischen und systematischen Kenntniss der Sipunculiden. Zeitschr. f. wiss. Zool., Bd. XV. Heft 4, pp. 404–445, Taf. XXXI.–XXXIII. .25. Oct., 1865.

Keferstein, W., und Ehlers, E.

'61. Zoologische Beiträge gesammelt im Winter 1859–60 in Neapel und Messina. II. Untersuchungen über die Anatomie des Sipunculus nudus. pp. 35–52, Taf. VI.–VIII. Leipzig, 1861.

Leydig, F.

'61. Die Augen und neue Sinnesorgane der Egel. Arch. f. Anat. u. Physiol., 1861, pp. 588–605.

Nansen, F.

'87. The Structure and Combination of the Histological Elements of the Central Nervous System. Bergens Museums Aarsberetning for 1886, pp. 29–215, Pl I.–XI.

Rietsch, M.

'86. Étude sur les Géphyriens armés ou Echiuriens. 1re et 2me Partie. Recueil Zool. Suisse, Tom. III. pp. 313–515, Pl. XVII.–XXII. Juin–Juillet, 1886.

Rohde, E.

'87. Histologische Untersuchungen über das Nervensystem der Chaetopoden. Zool. Beiträge (Schneider's), Bd. II. Heft 1, pp. 1–81, Taf. I.–VII.

Selenka, E.

'83. Die Sipunculiden, eine systematische Monographie. Semper's Reisen in den Philippinen, II. Theil, Bd. IV., 131 pp., 14 Pls. Wiesbaden, 1883.

Shipley, A. E.

'90. On Phymosoma varians. Quart. Jour. Micr. Sci., Vol. XXXI. pp. 1–27, Pl. I.–IV. April, 1890.

'91. On a New Species of Phymosoma, with a Synopsis of the Genus and some Account of its Geographical Distribution. Quart. Jour. Micr. Sci., Vol. XXXII. pp. 111–126, Pl. XI. March, 1891.

Spengel, J. W.

'77. Anatomische Mittheilungen über Gephyreen. Amtlicher Bericht der 50. Versammlung deutscher Naturforscher und Aerzte in München vom 17. bis 22. Sept., 1877. p. 189.

'80. Beiträge zur Kenntnis der Gephyreen. II. Die Organisation des Echiurus Pallasii. Zeitschr. f. wiss. Zool., Bd. XXXIV. Heft 3, pp. 460–538, Taf. XXIII.–XXVI. 30. Juli, 1880.

'81. Oligognathus Bonelliæ, eine schmarotzende Eunicee. Mitth. aus d. Zool. Station Neapel, Bd. III. Heft 1, pp. 15–52, Taf. II.–IV. 9. December, 1881.

Vogt, C., und Yung, É.

'88. Lehrbuch der praktischen vergleichenden Anatomie. Bd. I., 906 pp., mit 425 Holzschnitten. Viehweg und Sohn, Braunschweig, 1888.

EXPLANATION OF FIGURES.

All figures were drawn with the aid of an Abbé camera, unless otherwise stated. They represent without exception preparations of *Sipunculus nudus*, L. The method of staining and systems employed are indicated briefly for each specimen.

ABBREVIATIONS.

can. o. ceb.	Canal of cerebral organ.
cl. gn. I., II., III.	Ganglionic cell I., II., or III.
cl. fil.	Filamentous hypoderm cell.
cl. pig.	Pigment cell.
cl. sns.	Sensory cell.
coms. a.	Anterior commissure of brain.
coms. d.	Dorsal “ “
coms. œ.	Œsophageal connective.
coms. v.	Ventral commissure of brain.
con't. tis.	Connective tissue.
cps. enc.	Capsule of brain.
crnu. d.	Dorsal horn of tentacular fold.
ct.	Cutis.
cta.	Cuticula.
gl.″	Bicellular gland.
gl.″ dt.	Duct of bicellular gland.
gl.″ env.	Envelope “ “
gl.″ nl.	Nucleus “ “
gl.″ vl.	Vacuole “ “
gl.‴	Multicellular gland.
gl.‴ dt.	Duct of multicellular gland.
gl.‴ env.	Envelope “ “
gl.‴ n. fbr.′	Nervous fibrilla to multicellular gland.
gl.‴ nl.	Nucleus of the multicellular gland.
gn. su'œ.	Supraœsophageal ganglion.
h'drm.	Hypodermis.
leu'cy.	Leucocytes.
mb. ba.	Basement membrane.
mit.	Mitome.
mu. crc.	Circular muscles.
n'gl.	Neuroglia.
n'gi. nl.	Neuroglia nucleus.
n. mu. ret.	Nerve of retractors.
nl. sns.	Nucleus of sensory cell.
n. spl.	Splanchnic nerve.
n. ta.	Tentacular nerve.
o. ceb.	Cerebral organ.
or.	Mouth.
pa'mit.	Paramitome.
pap.	Papilla.
pli. ta.	Tentacular fold.
plx. n. drm.	Dermal nerve plexus.
pr'c. dg.	Digitate processes of brain.
rm. gl.	Glandular branch of plexus.
rm. mu.	Muscular “ “
spht.	Sphincter of cerebral canal.
va. sng. d.	Dorsal blood-vessel.
va. sng. v.	Ventral blood-vessel.
z. lev.	Smooth zone of introvert.
z. pap. a.	Anterior papillate zone of introvert.
z. pap. p.	Posterior papillate zone of introvert.

PLATE I.

Fig. 1. Anterior half of the introvert. The base of the figure corresponds to the middle of the posterior papillate zone. The slight contraction at the centre of the zona levis is not usually found. Camera outline. Simple microscope. × 3.

" 2. Anterior aspect of tentacular fold. The figure is diagrammatic only to the extent that secondary folds are omitted. Camera outline. Simple microscope. × 4.

" 3. Sagittal section of introvert. Diagrammatic in regard to details. Simple microscope. × 8.

" 4. Longitudinal section of body wall of introvert in the anterior portion of the posterior papillate zone. Muscles diagrammatic. Böhmer's hæmatoxylin. Zeiss 3. A. × 98.

" 5. Transverse section of body wall at about the region indicated by the line *gl.''* in Fig. 4. Hamann's carmine. Zeiss 1. D. × 370.

" 6–8. Sections of bicellular glands in the three dimensions of space. Kleinenberg's hæmatoxylin. Zeiss apochr. 4 mm. Oc. 6. × 425.

" 6. Soon after the beginning of secretion. The membrane dividing the two cells is shown at *.

" 7. At the period of greatest activity in secretion.

" 8. At the close of secretive activity.

" 9. Transverse section of duct of bicellular gland immediately below the cuticula. Zeiss apochr. 4 mm. Oc. 6. × 425.

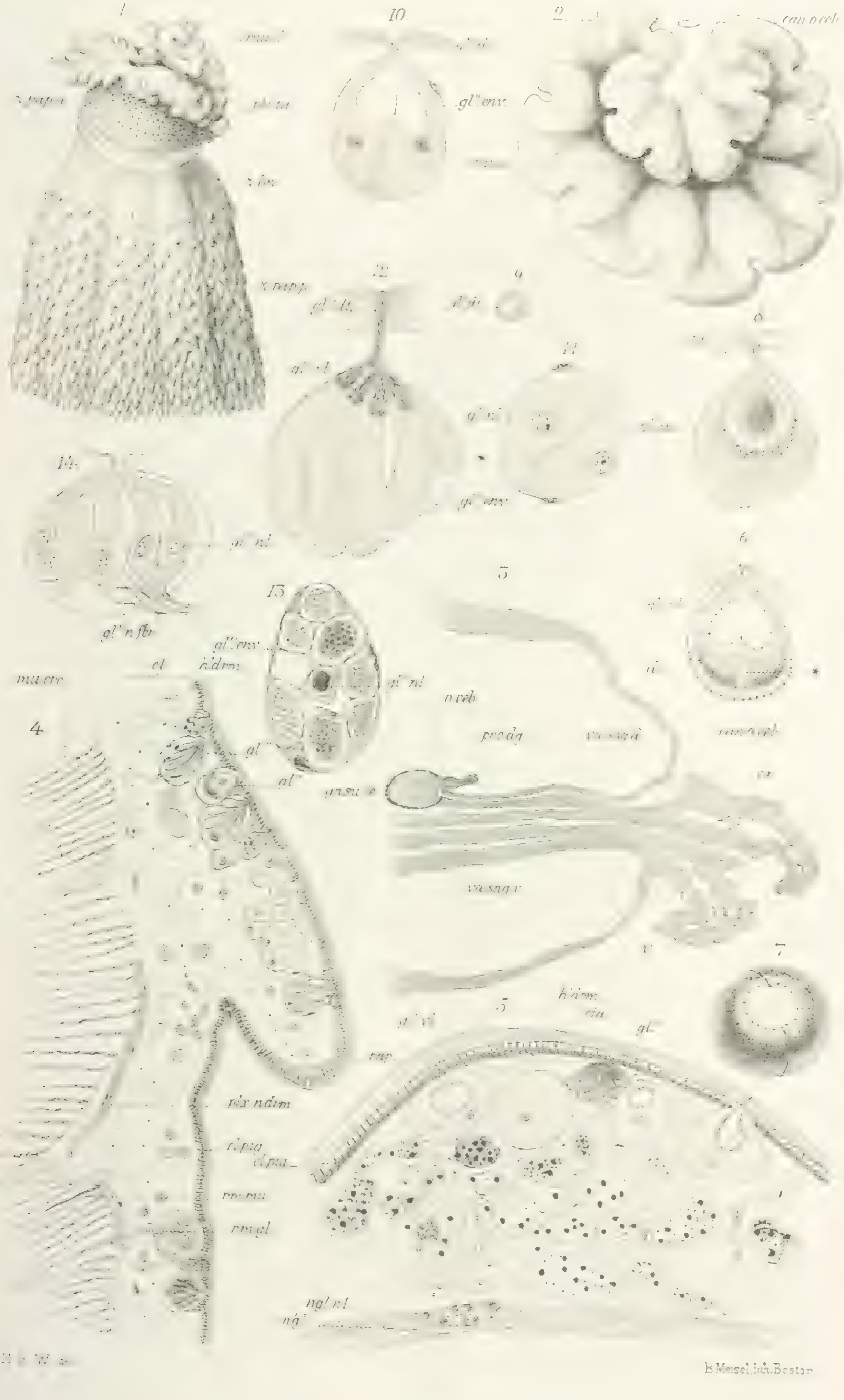
" 10, 11. Longitudinal and transverse sections of bicellular glands to demonstrate position of nuclei. Hamann's carmine. Zeiss apochr. 4 mm. Oc. 6. × 425.

" 12–14. Multicellular glands. Zeiss apochr. 4 mm. Oc. 6. × 400.

" 12. Longitudinal section. The duct is filled with a secreted material. Kleinenberg's hæmatoxylin.

" 13. Transverse section. At the left centre of the section a cell has fallen out. Hamann's carmine.

" 14. Longitudinal section to demonstrate nuclei and connection of gland cells with nerve fibres. Mayer's cochineal.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B. Meisel lith. Boston

PLATE II.

Fig. 15. Transverse section of epithelium of tentacular fold to show the leucocytes *in situ*. Hamann's carmine. Zeiss 1. E. × 500.

" 16–18. Sense papillæ from anterior papillate zone of introvert.

" 16. Tangential section through a single papilla. Hamann's carmine. Zeiss 1. D. × 300.

" 17. Transverse section. Apical area retracted. Hamann's carmine. Zeiss 1. D. × 330.

" 18. Transverse section. Papilla fully expanded. Orth's picro-litho-carmine. Zeiss 1. D. × 220.

" 19. Lateral sagittal section of brain at point of departure of the anterior commissure from the central fibrous mass. Plane of section indicated on Figure 22 by dotted line "19." Mayer's cochineal. Zeiss 1. A. × 50.

" 20. Median sagittal section of brain. Plane of section indicated on Figure 22. Mayer's cochineal. Zeiss 1. A. × 50.

" 21. Cells of tentacular epithelium isolated by maceration; *a*, *c*, and *e*, sensory, *b*, *d*, and *f*, filamentous cells. Zeiss apochr. 4 mm. Oc. 8. × 725.

" 22. Central nervous system. Composite figure from maceration preparations controlled by serial sections. The splanchnic nerve (*n. spl.*) should project *forward* under the brain. For the sake of clearness it is represented as if turned posteriad; * denotes inferior muscular branch (?). The numbers denote the planes of sections represented in Figures 19, 20, 24, and 25. × 8 (about).

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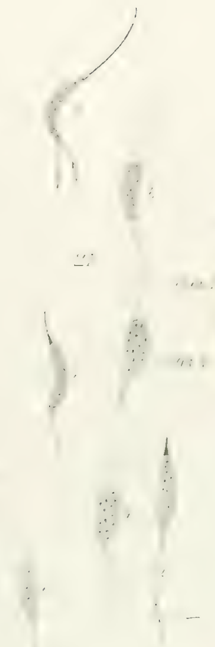

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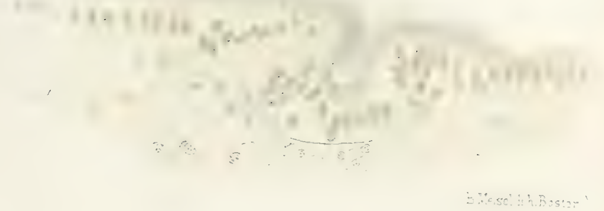

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PLATE III.

Fig. 23. Transverse section of hypodermis of tentacular fold with sensory cells. Weigert's picro-carmine. Zeiss apochr. 4 mm. Oc. 8. × 725.

" 24. Transverse section of brain. Plane of section shown in Figure 22, Plate II Grenacher's alcoholic borax carmine. Zeiss 1. A. × 50.

" 25. Transverse section of brain. Plane of section shown in Figure 22, Plate II. The section was cut somewhat obliquely, and the right half lies posteriad. Grenacher's alcoholic borax carmine. Zeiss 1. A. × 50.

" 26. Transverse section of body wall passing through the canal of the cerebral organ at about the middle of its course. The left of the figure is dorsal. Hamann's carmine Zeiss 1. A. × 50.

" 27. Transverse section of the cerebral organ: only one half is represented, and but a small section is drawn in detail. The cerebral canal begins at the angle near the number 27, and extends forward at right angles to the surface marked *cta.* The transition from the cuticula of the cerebral organ to that of the canal is marked by a †. Czokor's cochineal and picric acid. Zeiss apochr. 4 mm. Oc. 8. × 510.

" 28–31. Ganglionic cells. Zeiss apochr. 4 mm. Oc. 8. × 510. Fig. 28, Class III. Fig. 29, Class II. Fig. 30, Nuclei of Class I. Fig. 31, Class I.

" 32. Oblique section through a ganglionic cell of Class II., showing the regular arrangement of the paramitone. Hamann's carmine. Zeiss apochr. 4 mm. Oc. 8. × 725.

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B. Meisel, lith. Boston

No. 4. — *Three Letters from* ALEXANDER AGASSIZ *to the* HON. MARSHALL MCDONALD, *United States Commissioner of Fish and Fisheries, on the Dredging Operations off the West Coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of* ALEXANDER AGASSIZ, *carried on by the U. S. Fish Commission Steamer "Albatross,"* LIEUT. COMMANDER Z. L. TANNER, U. S. N., *Commanding.*

I.

STEAMER ALBATROSS, PANAMA, U. S. OF COLOMBIA,
March 14, 1891.

MY DEAR COLONEL MCDONALD: —

We returned yesterday from our first trip. The route extended from Panama to Point Mala, and next to Cocos Island; from there we ran in a southerly direction, then northwesterly to Malpelo Island, and back to the hundred-fathom line off the Bay of Panama. We spent several days trawling off the continental plateau of the Bay. This trip being rather in the nature of a feeler, I cannot tell you just what I think it means. But I believe I can to some extent conjecture probabilities from what has been accomplished.

I have found, in the first place, a great many of my old West Indian friends. In nearly all the groups of marine forms among the Fishes, Crustacea, Worms, Mollusks, Echinoderms, and Polyps, we have found familiar West Indian types or east coast forms, and have also found quite a number of forms whose wide geographical distribution was already known, and is now extended to the Eastern Pacific. This was naturally to be expected from the fact that the district we are exploring is practically a new field, nothing having been done except what the "Albatross" herself has accomplished along the west coast of North and South America. The "Challenger," as you will remember, came from Japan to the Sandwich Islands, and from there south across to Juan Fernandez, leaving, as it were, a huge field of which we are attacking the middle wedge. As far as we have gone, it seems very evident that, even in deep water, there is on this west coast of Central America a considerable fauna which finds its parallel in the West Indies, and recalls the precretaceous times when the Caribbean Sea was practically a bay of the Pacific. There are, indeed, a number of genera in the deep water, and to some extent also in the shallower depths, which show far greater affinity with the Pacific than with the Atlantic fauna. Of course, further exploration may show that some of these genera are simply genera of a wider geographical distribution; but I think a sufficiently large portion of the deep-sea fauna will still attest the former connection of the Pacific and the Atlantic.

I am thus far somewhat disappointed in the richness of the deep sea fauna in the Panamic district. It certainly does not compare with that of the West Indian or Eastern United States side. I have little doubt that this comparative poverty is due to the absence of a great oceanic current like the Gulf Stream, bringing with it on its surface a large amount of food which serves to supply the deep-sea fauna along its course. In the regions we have explored up to this time, currents from the north and from the south meet, and then are diverted to a westerly direction, forming a sort of current doldrums, turning west or east or south or north according to the direction of the prevailing wind. The amount of food which these currents carry is small compared with that drifting along the course of the Gulf Stream. I was also greatly surprised at the poverty of the surface fauna. Except on one occasion, when during a calm we passed through a large field of floating surface material, we usually encountered very little. It is composed mainly of Salpæ, Doliolum, Sagittas, and a few Siphonophores, — a striking contrast to the wealth of the surface fauna to be met with in a calm day in the Gulf of Mexico near the Tortugas, or in the main current of the Gulf Stream as it sweeps by the Florida Reef or the Cuban coast near Havana. We also found great difficulty in trawling, owing to the considerable irregularities of the bottom. When trawling from north to south, we seemed to cut across submarine ridges, and it was only while trawling from east to west that we generally maintained a fairly uniform depth. During the first cruise we made nearly fifty hauls of the trawl, and in addition several stations were occupied in trawling at intermediate depths. In my dredgings in the Gulf of Mexico, off the West Indies, and in the Caribbean, my attention had already been called to the immense amount of vegetable matter dredged up from a depth of over 1,500 fathoms, on the lee side of the West India Islands. But in none of the dredgings we made on the Atlantic side of the Isthmus did we come upon such masses of decomposed vegetable matter as we found on this expedition. There was hardly a haul taken which did not supply a large quantity of water logged wood, and more or less fresh twigs, leaves, seeds, and fruits, in all possible stages of decomposition. This was especially noteworthy in the line from the mainland to Cocos Island, and certainly offers a very practical object lesson regarding the manner in which that island must have received its vegetable products. It is only about 275 miles from the mainland, and its flora, so similar to that of the adjacent coast, tells its own story. Malpelo, on the contrary, which is an inaccessible rock with vertical sides, and destitute of any soil formed from the disintegration of the rocks, has remained comparatively barren, in spite of its closer proximity to the mainland.

The most interesting things we have found up to this time are representatives of the Ceratias group of Fishes, which the naturalists of the "Albatross" tell me they have not met before on the west coast of North America. The Crustacea have supplied us with a most remarkable type of the Willemoesia group. The paucity of Mollusks and also of Echini is most striking, although we brought up in one of the hauls numerous fragments of what must have been a gigantic species of Cystechinus, which I hope I may reconstruct. We were also fortunate enough to find a single specimen of Calamocrinus off Morro Puercos, in 700 fathoms, a part of the stem with the base, showing its mode of attachment to be similar to that of the fossil Apiocrinidæ. The number of Ophiurans was remarkably small as compared with the fauna of deep waters on the Atlantic side, where it often seems as if Ophiurans had been the first and only objects created. The absence of deep-sea corals is also quite striking. They play so important a part in the fauna of the deeper waters of the West Indies, that the contrast is most marked. Gorgoniæ and other Halcyonoids are likewise uncommon. We have found but few Siliceous Sponges, and all of well known types. Starfishes are abundant, and are as well represented in the variety of genera and species as on the Atlantic side of the Isthmus. I may also mention the large number of deep-sea Holothurians (Elasipoda) which we obtained, as well as a most remarkable deep-sea Actinian, closely allied to Cerianthus, but evidently belonging to a new family of that group. We found the usual types of deep-sea West Indian Annelids, occasionally sweeping over large tracts of mud tubes in the region of green mud. Although we dredged frequently in most characteristic Globigerina ooze, I was much struck with the absence of living Globigerinæ on the surface. Only on two occasions during a calm did we come across any number of surface Globigerinæ and Orbulinæ. On one occasion the trawl came up literally filled with masses of a species of Rhabdamina closely allied to R. lineata. Thus far no pelagic Algæ have been met with.

It is interesting to note that at two localities we came across patches of modern greensand similar in formation to the patches discovered off the east coast of the United States by the earlier dredgings of the Coast Survey, of Pourtalès, and of the "Blake." Having always been more or less interested in pelagic faunæ, and having paid considerable attention to its vertical distribution during my earlier cruises in the "Blake," I was naturally anxious to reconcile the conflicting statements and experiences of the naturalists of the "Challenger" and "Gazelle" on one side, and my own observations on the other. Both Murray and Studer contended that, in addition to the deep-sea and pelagic faunæ, there was what might be called an intermediate fauna with characteristic species, having nothing in common with the other two; while I maintained, on the other hand, from my experiments in the "Blake," that there was no such intermediate fauna, but that the pelagic fauna might descend to a considerable depth during the daytime to escape the effects of light, heat, and the disturbing influence of surface winds, and that this surface fauna on the Atlantic side — off shore in deep water — did not descend much deeper than 150 to 200 fathoms. In order to test this point, Dr. Chun, under the auspices of the Naples Station, made an expedition to the Ponza Islands. Dr. Chun applied to a tow-net an apparatus for closing it, similar to the propeller in use on our thermometer and water cups. He towed to a depth of 1,400 meters, if I am not mistaken, but never at any great distance from the mainland or from the islands of the Gulf of Naples, and came to the conclusion that the pelagic fauna existed all the way to the bottom. At the time, I considered his experiments inconclusive, and was of course anxious to repeat them in a strictly oceanic district, in great depths, and at a considerable distance from shore. I had an apparatus constructed by Ballauf of Washington, similar to that used by Dr. Chun. Unfortunately, in testing it we found the pressure of the tow-net against the propeller shaft so great as to make the machine useless, or at any rate, most unreliable. Thanks to the ingenuity of Captain Tanner, we overcame these obstacles. He devised a net which could be closed at any depth by a messenger, and which worked to perfection at 200, 400, 300, and 1,000 fathoms, and had the great advantage of bringing up anything it might find on its way up above the level at which it was towed. The lower part of the bag alone was closed by a double set of slings pulled by two weights liberated from a bell crank by a messenger. We found that, in towing the net at 200 fathoms for twenty minutes, we got everything in any way characteristic of the surface fauna which we had fished up with the tow-net at the surface. In addition to this, we brought up five species of so called deep-sea Fishes, Scopelus, Gonostoma, Beryx, and two others, which had thus far been brought up in the trawl, and considered characteristic of deep water. Also a peculiar Amphipod, and the young of the new species of Willemoesia mentioned above. We then tried the same net at 300 and 400 fathoms, and in neither case did we bring up anything in the closed part of the bag, while the upper open part brought up just what we had found previously at a depth of 200 fathoms, plainly showing that in this district the surface fauna goes down to a depth of 200 fathoms, and no farther. Next came our single attempt to bring up what might be found, say within 100 fathoms of the bottom, and Captain Tanner's net was towed at a depth of 1,000 fathoms where the soundings recorded 1,100. Unfortunately, we deepened our water while towing only twenty minutes to over 1,400 fathoms, so that we failed in our exact object. But we brought up in the closed part of the bag two species of Crustacea, a Macruran and an Amphipod, both entirely unlike anything we had obtained before. I hope in the next cruise to follow this up, and determine also the upper limits of the free-swimming deep-sea fauna. In the upper part of the bag (the open part) we brought up a couple of so called deep-sea Medusæ, which must have been collected at a comparatively moderate depth, judging from their perfect state of preservation.

I can hardly express my satisfaction at having the opportunity to carry on this deep-sea work on the "Albatross." While of course I knew in a general way the great facilities the ship afforded, I did not fully realize the capacity of the equipment until I came to make use of it myself. I could not but contrast the luxurious and thoroughly convenient appointments of the "Albatross" with my previous experiences. The laboratory, with its ingenious arrangements and its excellent accommodations for work by day and by night, was to me a revelation. The assistance of Messrs. Townsend and Miller in the care of the specimens was most welcome, giving me ample time to examine the specimens during the process of assorting them, and to make such notes as I could between successive hauls, while paying some attention also to the work of the artist, Mr. Westergren. He has found his time fully occupied, and we have in this trip brought together a considerable number of colored drawings, giving an excellent general idea of the appearance of the inhabitants of the deep waters as they first come up. These drawings can be used to great advantage with the specimens in making the final illustrations to accompany the reports of the specialists who may have charge of working up the different departments. . . .

We left Panama on the 22d of February, and returned to Panama after an absence of twenty days.

II.

Albatross, Acapulco, April 14, 1891.

We have reached the end of our second line of explorations. After coaling we left Panama, and reached Galera Point, where we began our line across the Humboldt Current, which was to give us a fair idea of the fauna of that part of the coast as far as the southern face of the Galapagos. With the exception of three good casts, the trawling on that part of the sea bottom proved comparatively poor, nor did the sea face of the southern slope of the Galapagos give us anything like the rich fauna I had expected. Theoretically, it seemed certain that a sea face like that of the Galapagos, bathed as it is by a great current coming from the south and impinging upon its slope, and carrying upon its surface a mass of animal food, could not fail to constitute a most favorable set of conditions for the subsistence and development of a rich deep-sea fauna.

In the deeper parts of the channel between Galera Point and the southern face of Chatham Island we found a great number of Elasipoda, among them several genera like Peniagone, Bathodytes, and Euphrosine, represented by numerous species. The Starfishes of this our second cruise did not differ materially from those collected during our first trip, but we added some fine species of Freyella, Hymenaster, Astrogonium, Asterina, and Archasteridæ to our collections. Among the Sea-urchins on two occasions we brought up fine hauls of a species of Cystechinus with a hard test, many specimens of which were in admirable state of preservation. Among the Ophiurans nothing of importance was added, unless I may except a lot of Ophiocreas attached to a Primnoa, and a pretty species of Sigsbea attached to a species of Allopora, from the south side of Chatham Island.

The Gorgonians were remarkably few in number, which is undoubtedly due to the unfavorable nature of the bottom we worked upon. Nearly everywhere except on the face of the Galapagos slope we trawled upon a bottom either muddy or composed of Globigerina ooze, more or less contaminated with terrestrial deposits, and frequently covered with a great amount of decayed vegetable matter. We scarcely made a single haul of the trawl which did not bring up a considerable amount of decayed vegetable matter, and frequently logs, branches, twigs, seeds, leaves, fruits, much as during our first cruise.

Our Crustaceans, from the nature of the bottom, naturally consisted of the same groups of deep-sea types which we obtained before. I may, however, mention a haul containing a goodly number of Nephrops, a genus we had not previously obtained.

Among the Worms the Maldaniæ and limicolous types were unusually abundant at some localities, the empty mud tubes often filling the bottom of the trawl. Some very large specimens of Trophonia were collected, and remarkably brilliantly colored (orange and carmine) Nemerteans and Planarians.

The Mollusks were very scanty, and the absence of Comatulæ or other Crinoids was equally disappointing, even when trawling on the extension of the line started three years ago by the "Albatross," on the eastern face of the Galapagos slope, when on her way from Chatham Island to San Francisco. We took up this line off Indefatigable Island, hoping to obtain from that quarter our best results, but our hauls were very disappointing. The ground proved not only most difficult to dredge upon, but also comparatively barren, and it was not till we got into the oceanic basin again, between the Galapagos and Acapulco, that our catches improved. But even then they were not to be compared with the hauls at similar depths in the Atlantic off the West Indies, or along the course of the Gulf Stream.

Among the Fishes, our most important catches were fine specimens of Bathyonus, of Bathybrissa, of Bathypteroides, and a few specimens of Ipnops in excellent condition.

From the nature of the bottom we naturally expected rich hauls of Siliceous Sponges, but we did not find many, and I do not think there are many novelties among those we have collected. On two occasions, a number of specimens of Ascidians were brought up; among them was a fine white translucent Corinascidia.

Among the Bryozoans, the most noteworthy haul was a number of beautiful specimens of the delicate Naresia, in excellent condition. On the line from the Galapagos to Acapulco we brought up a good many Foraminifera from the mud bottoms. On several occasions the bottom must have been covered with huge masses of a new type of an arenaceous Foraminifer, forming immense curling sheets attached by one edge to stones or sunk into the mud. This Foraminifer seems to increase in size by forming irregular more or less concentric crescent-shaped rings. When it comes to the surface, it is of a dark olive-green color.

During this second cruise we continued our experiments with the Tanner closing tow-net, in order to determine the lower limits of the surface pelagic fauna, and to determine also if there is any so called intermediate pelagic fauna at other depths, or within a short distance from the bottom.

On the 25th of March, at a point not quite half way between Cape San Francisco and the Galapagos, in 1,832 fathoms of water, the Tanner net was sent down to tow at a depth which varied from 1,739 to 1,773 fathoms. The net was towed within these limits for a period of something over twenty minutes. The messenger was then sent down to close the net; time occupied seven minutes. The net was then drawn up to the surface. The lower part of it was found to have closed perfectly, and contained nothing beyond a few fragments of leaves. The lower bag was carefully washed in water which had been strained, and the water examined with all possible care, and sifted again. It contained nothing. The upper part of the net, however, which had remained open on its way up, was found to contain the identical surface things which on former occasions we had found in the Tanner net down to a depth of 200 fathoms. They were a small species of Sagitta, and species of Doliolum, Appendicularia, a huge Sagitta, a large number of Leucifer and Sergestes, and several species of Schizopods and Copepods; two species of Hyperia, probably parasitic on a Salpa, which was also quite abundant; several finely colored Calanus, some Isopods, and a number of fragments of what must have been a very large Beroe, measuring from five to six inches in diameter; Leptocephalus, several specimens of Stomias, of Scopelus, of Melamphæs, and other species, many of which, like some of the Schizopods, had been considered as typical deep-sea forms. Among the so called deep-sea Medusæ, several specimens of Atolla and Periphylla were also found in the open part of the net. I may mention also as of special interest a huge Ostracod, allied to Crossophorus, with a thin semi-transparent carapace, and measuring somewhat more than one inch in length. The largest Ostracod previously known is not more than one third of an inch long. On two other occasions this same Ostracod was brought up in the tow-net from a depth of less than 200 fathoms.

The surface at this point was also examined with the tow-net, and the pelagic animals found to be the same as those brought up in the open part of the tow-net on its way from the bottom. The number both of species and specimens was, however, much less than in the Tanner net. On the following day the Tanner tow-net was sent to be towed at a depth of 214 fathoms. In twenty minutes the messenger was sent down and the net hauled up. The bottom part of the net came up tightly closed. Its contents were examined in the same manner as before in well sifted water, and the water was found to be absolutely barren, while the upper part of the net, which came up open, and was not more than eight or nine minutes on the way, was well filled with surface life. The net contained this time a number of Hyalæas and Criseis, in addition to the things collected the day before. An examination of the surface fauna at this same point with the tow-net showed the presence only in smaller numbers of the same species which the open part of the same net contained, except that there were a larger number of bells and fragments of Diphyes and of Cristalloides than in the Tanner net. The point at which this experiment was made was about 250 miles from the Galapagos, and about the same distance from Cape San Francisco. There were myriads of Nautilograpsus swarming on the surface of the water; they literally filled the surface tow-net. On two other occasions, once at a distance of 350 miles in a southeasterly direction from Acapulco (depth 2,232 fathoms), we tried the same experiment with the Tanner net, and invariably with the same result. The net was towed at a depth of 100, of 200, and of 300 fathoms, each time for twenty minutes, the messenger sent down, and the bottom part closed. At the depth of 100 fathoms, the closed part of the net contained practically the same things as the open part of the net; at 200 fathoms, the lower part of the net contained but few specimens of the surface life; and at 300 fathoms, the closed bottom net came up empty.

On the following day the surface was carefully examined, and the tow-net sent to 175 fathoms, where it was towed for twenty minutes, and the messenger sent down to close it. The lower net came up well filled with the surface pelagic species, which on this day were unusually varied, it having been smooth and calm the previous night, and the morning before the towing was made. This haul was made in the evening, at 8 P. M. The previous hauls had been made at about 10 A. M., in a brilliant sunlight. Again on the 11th of April, about thirty miles southeast of Acapulco, in a depth of over 1,800 fathoms, the Tanner net was sent to a depth of 300 fathoms, and the messenger sent down to close it.

There was nothing in the lower part of the net which had been closed, while the open part contained an unusually rich assortment of surface species, and among them a large number of Scopelus, of Schizopods, and of Rhizopods, mainly Collozoun and Acanthometra.

These experiments seem to prove conclusively that in the open sea, even when close to the land, the surface pelagic fauna does not descend beyond a depth of 200 fathoms, and that there is no intermediate pelagic fauna living between that depth and the bottom, and that even the free-swimming bottom species do not rise to any great distance, as we found no trace of anything within 60 fathoms from the bottom, where it had been fairly populated.

The experiments of Chun regarding the distribution of the pelagic fauna have all been made in the Mediterranean, within a comparatively short distance from the shore, and in a closed basin showing, as is well known, special physical conditions, its temperature to its greatest depths being considerably higher than the temperature of oceanic basins at the limit of 200 fathoms, or thereabout, which we assume now to be the limit of the bathymetrical range of the true oceanic pelagic fauna. At 200 fathoms our temperature was from 49° to 53°, while, as is well known, the temperature of the Mediterranean soon falls at 100 fathoms even to about 56°, a temperature which is continued to the bottom in this closed basin. Of course, if temperature is one of the factors affecting bathymetrical distribution, there is no reason except the absence of light which would prevent the surface pelagic fauna from finding conditions of temperature at the greatest depth similar to those which the surface fauna finds within the limit of 200 fathoms in an open oceanic basin.

Arriving as we did at the Galapagos at the beginning of a remarkably early rainy season, I could not help contrasting the green appearance of the slopes of the islands, covered as they were by a comparatively thick growth of bushes, shrubs, and trees, to the description given of them by Darwin, who represents them in the height of the dry season as the supreme expression of desolation and barrenness. Of course, here and there were extensive tracts on the sea-shore where there was nothing to be seen but blocks of volcanic ashes, with an occasional cactus standing in bold relief, or a series of mud volcanoes, or a huge black field of volcanic rocks, an ancient flow from some crater to the sea; but as a rule the larger islands presented wide areas of rich, fertile soil, suitable for cultivation. The experiments at Charles Island, where there is a deserted plantation, and at Chatham Island, where Mr. Cobos has under successful cultivation a large plantation producing sugar, coffee, and all the tropical fruits, as well as extensive tracts on which his herds of cattle, sheep, and donkeys roam towards the higher central parts of the island, show the fertility of these islands. They are indeed as favorably situated for cultivation as the Sandwich Islands or Mauritius, and there is no reason why, if properly managed, they should not in the near future yield to their owners as large returns as do those islands.

I obtained from Mr. Cobos a piece of the so called sandstone said to occur on Indefatigable Island, and which of course I was most anxious to see, as the occurrence of true sandstone would have put quite a different face on the geological history of the Galapagos from the one usually received. This I found to be nothing but coral rock limestone, either a breccia or slightly oölitic, identical with the formation found back of the beach at Wreck Bay on Chatham Island. I found there an old coral rock beach, extending on the flat behind the present beach, composed entirely of fragments of corals, of mollusks, and other invertebrates, cemented together into a moderately compact oölitic limestone, which when discolored, as it often is and turned gray, would readily be mistaken for sandstone. This coral rock is covered by just such a thin, ringing coating of limestone as characterizes the modern reef rock of other localities. On nearly all the islands there are a number of sandy beaches made up of decomposed fragments of corals and other invertebrates, and cemented together at or beyond high-water mark into the modern reef rock I have described. The coral is mainly made up of fragments of Pocillopora, which is found covering more or less extensive patches off these coral sand beaches, but which, as is well known, never forms true coral reef in the Panamic district. The only true coral reef belonging to this district is that of Clipperton Island, (if we can trust the Admiralty charts,) situated about 700 miles to the southwest of Acapulco. But neither at Cocos Island, nor at the Galapagos, nor anywhere in the Panamic district, do we find true coral reefs, — nothing but isolated patches of reef-building coral. The absence of coral reefs in this district has of course already been noted by other naturalists, who have been struck by this feature in an equatorial region. Dana has ascribed it to the lower temperature of the water due to the action of the Humboldt Current coming from the south, pouring into the Bay of Panama, and then flowing westward with the colder northerly current coming down the west coast of Mexico and Central America. From the investigations made this year by the "Albatross," I am more inclined to assume that the true cause of the absence of coral reefs on the west coast of Central America is due to the immense amount of silt which is brought down the hill and mountain sides every rainy season, and which simply covers the floor of the ocean to a very considerable distance from the land, the land deposits being found by us even on the line from the Galapagos to Acapulco at the most distant point from the shore to the side or extremities. The mud in Panama Bay to the hundred-fathom line is something extraordinary, and its influence on the growth of coral reefs is undoubtedly greatly increased from the large amount of decomposed vegetable matter which is mixed with the terrigenous deposits.

The course of the currents along the Mexican and the Central and South American coasts clearly indicates to us the sources from which the fauna and flora of the volcanic group of the Galapagos has derived its origin. The distance from the coast of Ecuador (Galera Point and Cape San Francisco) is in a direct line not much over 500 miles, and that from the Costa Rica coast but a little over 600 miles, and the bottom must be for its whole distance strewn thickly with vegetable matter. The force of the currents is very great, sometimes as much as 75 miles a day, so that seeds, fruits, masses of vegetation harboring small reptiles, or even large ones, as well as other terrestrial animals, need not be afloat long before they might safely be landed on the shores of the Galapagos. Its flora, as is well known, is eminently American, while its fauna at every point discloses its affinity to the Mexican, Central or South American, and even West Indian types, from which it has probably originated ; the last indicating, as well as so many of the marine types collected during this expedition, the close connection that once existed between the Panamic region and the Caribbean and Gulf of Mexico.

I have already referred to the physiognomy of the deep-sea fauna, showing relationship on the one side to Atlantic and West Indian types, and on the other to the extension of the Pacific types, which mix with the strictly deep-sea Panamic ones. The western and eastern Pacific fauna, while as a whole presenting very marked features in common, yet also present striking differences. The vast extent of territory over which some of the marine types extend, through all the tropical part of the Pacific, may readily be explained from the course of the great western equatorial current and the eastern counter current, which cannot fail to act as general distributors in space for the extension of a vast number of marine Vertebrates and Invertebrates.

Mr. Townsend made quite a large collection of Birds from Chatham and Charles Islands, considering the short time we were there.

As soon as we have reached Guaymas, I shall be able to give you a better *résumé* of the character of the deep-sea fauna of the Panamic region, and of its relationship on the one side to the Pacific fauna and on the other to the West Indian region.

III.

GUAYMAS, April 25, 1891.

We left Acapulco on the 15th of April, for our third cruise, into the Gulf of California, and steamed as far as Cape Corrientes without attempting to do any trawling. The character of the bottom, as indicated on the charts, promised nothing different from what we had dredged off Acapulco, and on the line from there to the Galapagos Islands. We made one haul off Cape Corrientes, bringing up nothing but mud and decomposed vegetable matter. This induced us to keep up the Gulf of California, till we were off the Tres Marias. We there made several hauls, and obtained some Umbellulæ, Pennatulæ, Trochoptilum, Anthoptilum, and a fine Antipathes, a few Comatulæ, a large Astropecten, some fine specimens of Urechinus and of Schizaster, a few Holothurians, Lophothuria, Trochostoma, and two species of Elasipoda, besides a few fragments of Gasteropods, with an empty shell of Argonauta.

Among the Crustacea there came up the usual types found living upon muddy bottom, such as Glyphocrangon, Heterocarpus, Notostoma, Pentacheles, Nematocarcinus, Nephrops, together with species of Lithodes and of Munida. The usual types of limicolous Annelid also were found here, Halinæcia, Terebella, Maldania, and the like, a few Ophiurans, Ophiopholis and Ophiocantha, a few fragments of Farrea, and a huge Hyalonema of the type of H. toxeres. Among the Fishes there were a few Macrurans, Bathypteroides, Lycodes, and Malthe. The trawl was usually well filled with mud, and with the mud came up the usual supply of logs, branches, twigs, and decayed vegetable matter.

On going farther north into the Gulf of California, the nature of the bottom did not change materially, and we found the trawling most difficult from the weight of the mud brought up in the trawl. But occasionally a haul was made which more than repaid us for the time spent on the less productive ones. Two of the hauls are specially worthy of mention, as being characteristic of the deep-water fauna of the Gulf of California, one made in 995 fathoms, and the other in 1,588 fathoms. We obtained in these hauls a number of Ophiomusium and Ophiocreas, some fine specimens of Schizaster, a new genus allied to Paleopneustes, and also the same species of Cystechinus, with a hard test, and of Phormosoma, which we had obtained before on the line from the Galapagos to Acapulco. Beside these, there came up a number of specimens of an interesting species of Pourtalesia, most closely allied to Pourtalesia miranda, the first type of the group dredged in the Florida Channel by Count Pourtalès.

The deeper haul was specially rich in Holothurians, among them a fine large white Cucumaria, some specimens of Trochostoma, several species of Bathodytes, some of them remarkable for their white color, their huge size, and comparatively small number of ventral tentacles. With these were numerous specimens of an interesting species of Euphronides. In this haul I was specially struck with the Elasipoda, and the great variety in the consistency of the skin in individuals of one and the same species; it varied in different individuals from extreme tenuity to a comparatively tough gelatine-like consistency. On carefully sifting the mud, we found a number of interesting Foraminifera, and of delicate and minute Gasterepods and Lamellibranchs, fragments of the shell of an Argonauta, and two species of a huge ribbed Dentalium. Among the Starfishes were specially noticeable a large Brisinga, a long-armed Cribrella, and several species of Astropecten. The usual types of Worms were found in the mud at these greater depths. In addition to a number of Macruroids, we obtained a pink Amphionus, a large black Beryx-like fish, a fine Nettastoma, and a couple of species of Lycodes. The usual surface species of Stomias and of Scopelus also came up in the trawl. Among the Crustaceans were a fine lot of Arcturus, of Colossendeis, of Glyphocrangon, and of a Caridid with a deep blue patch on the base of the carapace, making the strongest possible contrast to the dark crimson coloring of the rest of the body. Blue is a very unusual color in the deep-sea types, although the large eggs of some of the deep-sea Macrurans are often of a light blue tint.

We brought up in the trawl at various times, and subsequently also in the Tanner net, from depths of less than 200 fathoms, the same gigantic Ostracod which I mentioned in one of my previous letters, several specimens of Atolla, and fragments of a huge Periphylla, which must have been at least fifteen inches in diameter. Also a most interesting new type of Bougainvillia, remarkable for having eight clusters of marginal tentacles, but only four chymiferous tubes.

We continued our experiments with the Tanner tow-net. On the 16th of April, about 120 miles from Acapulco, we sent the net to tow at a depth of 175 fathoms, and after towing for about twenty minutes sent the messenger to close it. On examining the bottom part of the net, which came up tightly closed, we found it to contain practically the same things as we obtained in the surface net at the same spot.

On two occasions we sent the net to be towed at depths of 800 fathoms and of 700 fathoms, the depths at these points being in one case 905 fathoms and in the other 773 fathoms. At the greater depth, the water shoaled somewhat while towing, as the closed part of the net came up partly filled with fine silt; while during the second haul, the twisting of the swivel wound the straps of the weights round the rope, and the net came up open, but must have dragged very close to the bottom, as it contained a fine specimen of Nettastoma, and some Penæids, which we supposed to be deep-sea types. Otherwise the net contained only the customary surface species of Sagitta, Pteropods, Copepods, Schizopods, Tunicates, and Fishes. These two hauls were made about the middle of the Gulf of California, at a distance of some fifty miles in a southwesterly direction from Guaymas.

On the 23d of April, a few hours before reaching Guaymas, we made one more attempt with the Tanner tow-net, at a depth of 620 fathoms, sending the net to be towed at a depth of from 500 to 570 fathoms. We found in this case in the bottom part of the net, which came up tightly closed, a Scopelus, a Penæid, and a Hyalea, while the upper open part of the net contained the same surface species we had obtained before.

My experience in the Gulf of California with the Tanner self-closing net would seem to indicate that in a comparatively closed sea, at a small distance from the land, there may be a mixture of the surface species with the deep-sea bottom species, a condition of things which certainly does not exist at sea in an oceanic basin at a great distance from shore, where the surface pelagic fauna only descends to a comparatively small depth, about 200 fathoms, the limits of the depth at which light and heat produce any considerable variation in the physical condition of the water. The marked diminution in the number of species below 200 fathoms agrees fairly with the results of the "National" Expedition.

The more I see of the "Albatross," the more I become convinced that her true field is that of exploration. She is a remarkably fine sea boat, and has ample accommodation for a staff of working specialists such as would be needed on a distant expedition. The time will soon come when the Fish Commission will hardly care to continue to run her, and I can conceive of no better use for so fine a vessel than to explore a belt of 20° latitude north and south of the equator in the Pacific, from the west coast of Central America to the East Indian Archipelago.

The success of the "Albatross" thus far has depended entirely upon the zeal, energy, intelligence, forethought, and devotion of Captain Tanner, if I may judge of the past by the present. He never spares himself, and he is always ready to make the most of the time at his disposal for the benefit of the special object he has in charge. He looks after every haul of the trawl himself, and will not allow any one else to jeopard in any way the material of the vessel, or the time it requires to make a haul. That responsibility he assumes himself, and it constitutes his daily work. In looking over the records of the "Albatross" during her voyage from New York to San Francisco, I am struck with the amount of work which has been accomplished. It would be but a just return to Captain Tanner, if Congress would make the necessary appropriations to work up and publish all that he has brought together, not only on that cruise, but also what has been left untouched thus far of the immense collections made by him in the Caribbean, and off the east coast of the United States, to say nothing of his explorations in the Gulf of California, on the coast of California, on the coast of Alaska, and in the Behring Sea, from which he has accumulated endless and most interesting material, which no other ship could get together unless she had another Tanner in command.

We reached Guaymas on the 23d of April, in the afternoon, and I parted from the ship with great regret, but more than satisfied with the results of this expedition.

Allow me, in concluding, to thank you most cordially for having given me the opportunity to join the "Albatross" on this extended cruise, and for your kindness in urging the President to allow the vessel to be detailed for this work.

As soon as it may become practicable, I shall send you a full *résumé* of our work, accompanied with sketches of the Tanner tow-net and a detailed chart of the route we followed.

Very respectfully yours,

ALEXANDER AGASSIZ.

CAMBRIDGE, May, 1891.

No. 5. — *The Development of the Pronephros and Segmental Duct in Amphibia.* By Herbert H. Field.[1]

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I. Introduction.

The studies upon which this paper is based were undertaken with the purpose of determining the relation which the urogenital system bears to the germinal layers in Amphibia. At the time when they were begun, especial interest in this topic had been awakened by the appearance of Flemming's paper ('86), in which the author entirely confirmed the statement previously made by Graf Spee ('84), that the system was of ectodermal origin. This view was gladly welcomed on many sides, for it was felt that an origin from this source was more in harmony with general conclusions already accepted than was the method previously advocated. Moreover, a new light seemed now to be cast on the phylogeny of Vertebrates. Under these circumstances, it appeared highly desirable that the position which Graf Spee and Flemming had taken be subjected to the test of renewed investigation on other groups of Vertebrates than those employed by them. The researches of these authors had been conducted on Mammalian material only, and it was the hope of the writer to find in Amphibia a similar mode of origin for the excretory duct.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVII.

The material employed in the present investigations consisted of embryos of Rana, Bufo, and Amblystoma. The study of the problem was begun with Rana pipiens Schreb. (halecina), embryos of which had been prepared in the spring of 1884 by Prof. E. L. Mark, who kindly placed his series at my disposal. In the spring of 1889, while in Baltimore, Md., I secured an abundance of the eggs of Rana sylvatica Le Conte.[1] These eggs are large, measuring at the blastula stage two millimeters or more in diameter. I also found them far better for embryological study than those of other species of frogs examined. An advantage which they possess for my purpose is that the germ layers are very well separated from one another. Moreover, the body cavity appears at an early stage, making the boundary between the somatic and the splanchnic mesoderm very pronounced, both in the region of the protovertebræ and of the lateral plates.

The eggs of Bufo studied, B. americanus Le Conte, were collected during the spring of 1887, in Cambridge and in Jamaica Plain, Mass. At this time I also collected a small quantity of Amblystoma eggs from a pond in Jamaica Plain; but a careful search, carried on during several subsequent trips to this locality, failed to yield any more eggs.

Prof. J. S. Kingsley at this time kindly sent me from Indiana some Amblystoma material which he had preserved; but for the determination of many points at issue I was obliged to wait till another season offered opportunities for collection. In the spring of 1889, therefore, I made a trip to Baltimore, where I was able to collect an abundant supply of the eggs of this Amphibian, most if not all of the material collected belonging to the species A. punctatum Linn. In this work I was accommodated at the Biological Laboratory of the Johns Hopkins University, — a privilege for which I am under obligation to that institution. My thanks are particularly due my friend Dr. T. H. Morgan for his kind assistance during my stay in Baltimore, and for material of his collection.

I may here also express my obligations to Dr. John S. Billings, Surgeon U. S. Army, for the favor of sending me from the Surgeon General's library in Washington a number of papers to which I should otherwise have been unable to gain access. I am further indebted to Mr. Samuel Garman and to Mr. G. H. Parker for the revision of my proof-sheets, and for suggestions during the progress of my work. Mr. Parker also read the earlier portions of my manuscript.

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[1] Inasmuch as the observations of European investigators have usually been made on R. temporaria, it is of interest to note that R. sylvatica Le Conte has been regarded by some systematists as a variety of R. temporaria (Günther, '58, p. 17). In any event, the development of the two forms may be assumed to be very similar.

The material was prepared by ordinary histological methods; but inasmuch as many of the hardening reagents and stains which I tried gave thoroughly unsatisfactory results, I may state in brief the treatment which proved most successful. The embryos of both Rana and Bufo can be satisfactorily killed in Kleinenberg's picrosulphuric mixture; they can then be successfully stained in Orth's lithium-picrocarmin. The object should be exposed to the action of the stain as long as possible, care being taken to guard against maceration. In order to accomplish this purpose, it has frequently proved advantageous to stain the object twice, removing it after the first staining to strong alcohol. In passing the stained object through grades of alcohol, it is important to keep a little picric acid dissolved in the several fluids in order to prevent the alcohol from extracting the yellow stain from the specimen. Embryos treated in this way show a very effective double stain. The nuclei are bright carmine, contrasting with the yellow color imparted by the picric acid to the yolk spherules among which they are found. As a killing reagent, Merkel's fluid also gives good results. It should be followed by Kleinenberg's hæmatoxylin, and the decolorizing should be watched with care.

With Amblystoma the best method of treatment is that with Fol's chromic-osmic-acetic mixture, followed by Czokor's cochineal. The picrosulphuric mixture followed by picrocarmin, as recommended for Rana and Bufo, is also of service.

It is usually best to stain on the slide; and, in my experience, satisfactory results with hæmatoxylin can very rarely be reached by staining *in toto*.

II. Descriptive Part.

In the following account of the development of the pronephros and segmental duct, I shall first treat these organs descriptively. For this purpose, I shall take up in succession Rana, Bufo, and Amblystoma, and shall describe selected stages in the development of each. This account will be followed by a general discussion of nephridial organs, in which the results of other investigators will be reviewed.

A. Rana.

STAGE I.

Plate I. Figs. 1-3.

At the first stage which I shall describe the embryo has departed only a little from the spheroidal form presented by the egg during segmentation. The medullary plate is widely open, its lateral margins being only slightly elevated above the general surface. At the hinder end of the medullary plate the blastopore is plainly visible. An idea of the external form of the embryo can be gained by reference to Goette's figure of Bombinator ('75, Taf. III. Fig. 41), or to van Bambeke's of the Axolotyl ('80, Pl. XII. Fig. 9). In water of 15 to 18° C. eggs of R. sylvatica reached this stage in about sixty hours after fertilization; the eggs of R. halecina develop somewhat more slowly.

The general relations of the germinal layers at this stage are shown in Figure 2. The ectoderm consists of two distinct layers (Figs. 3 and 7, *ec'drm.'* and *ec'drm.''*). Except in the region of the medullary thickening (*la. med.*), which is produced by a proliferation of the deeper of these two layers, the ectoderm is nearly uniform in thickness. The two layers present slightly different histological characters. In the outer layer (Figs. 3 and 7, *ec'drm.'*) the cells are large and columnar, and their external surfaces project as rounded eminences, giving a roughly granular appearance to the surface of the embryo. Each cell contains scattered pigment granules, which are especially massed along its external face. Small yolk spherules (*sph. vt.*) are present in considerable numbers. The cells of the deep layer (*ec'drm.''*) are smaller than those of the outer, and are somewhat flattened. The pigment granules are scattered throughout the cells of this layer, without showing special accumulations. The yolk spherules present the same appearance as those of the superficial layer.

The entoderm and yolk cells (Fig. 2, *en'drm.* and *cl. vt.*) form the great mass of the interior of the embryo. The wide lumen of the gut traverses the dorsal portion of this mass. The chorda (*n'cd.*) has the form of a longitudinal ridge, imperfectly cut off from the entoderm below, and in contact with the medullary plate above. A single cell layer (*en'drm.*) on each side of the chorda forms the dorsal roof of the intestine. As this layer passes out laterally, it increases in thickness, becomes several cells deep, and finally merges in the mass of large yolk cells (*cl. vt.*) lying ventral to the intestinal cavity. All the cells of the entoderm contain large yolk spherules. Pigment is present in considerable quantity in the cells bordering the cavity of the intestine; elsewhere it occurs only as scattered granules.

At this stage two plates of mesoderm (Fig. 2, *la. ms'drm.*) extend out laterally, one on each side of the chorda, and pass ventrally around the mass of yolk cells to be united in the median line below. Each plate is thickest (Figs. 1, 3, at *la. pr'vr.*) next the notochord; as it passes outward, it becomes thinner. Before the ventral surface of the embryo is reached, it is reduced to a layer two cells thick, representing the somatopleure and splanchnopleure (*so'plu.* and *spl'plu.*) of this region. The cells of the mesoderm are in general smaller than those of the yolk-entoderm. The yolk spherules which they contain are also somewhat smaller than those in the entoderm. Pigment is rarely present except in the form of scattered granules.

In the foregoing account of the relations of the germ layers the description refers in the main to the typical condition, realized in the middle trunk region; in this and in subsequent stages modifications occur in the head and tail regions. These special conditions are of no consequence for the present purpose.

There are certain histological characters, to which allusion has already been made, which may serve as criteria for distinguishing the germ layers. The most satisfactory of these is the size of the yolk spherules. As I have indicated, the spherules are largest in the entoderm and smallest in the ectoderm; in the mesoderm they are of an intermediate size. Measurements of spherules from the three layers in the region of the future pronephros gave the following results: entoderm, mean diameter of spherules, $8\,\mu$; mesoderm, mean diameter, $5\,\mu$; ectoderm, diameter rarely exceeds $3\,\mu$. Excluding the head and tail regions, these dimensions represent, I believe, fair averages for the whole body. The distribution of pigment affords another criterion for distinguishing the layers. In the superficial ectoderm, the pigment (Figs. 3, 7) is massed along the external surface of each cell. In the deep ectoderm, it is present in considerable quantity, but is scattered throughout the cell. Except in certain specialized regions, there is little pigment in either mesoderm or entoderm. I have also noted the differences in the mean sizes of the cells: the yolk cells are in general the largest, and those of the ectoderm the smallest, the mesodermal cells being of intermediate size. The great variability of this character prevents its having much weight, however, in determining to which of the three layers a given group of cells belongs.

I shall now consider in greater detail some of the modifications which the mesoderm exhibits, particularly such as occur in the region where the pronephros is subsequently developed. For this purpose I have selected two embryos of Stage I. which show slightly different conditions. The account will first relate to the specimen which is shown, by the less differentiation of the medullary plate as well as by other features, to be the younger. This embryo measures 2.31 mm. in length. In following a series of cross sections forwards, the three germ layers become apparent at about 0.35 mm. from the posterior end, or a short distance in front of the blastopore. Here the structure of the mesoderm is rather obscure, since in a transverse section of the animal this layer is cut obliquely. The condition, however, is here nearly the same as that which I am about to describe for a more anterior section.

Figure 3 represents a section of this embryo 0.91 mm. from the posterior end. On the ventral side of the embryo the mesoderm consists of two layers, each of which is only a single cell in thickness. These two layers, which represent somatopleure and splanchnopleure, are separated by a narrow space, the cœlom (*cœl.*). In the lower left-hand corner of the figure, the beginning of this two-layered condition of the mesoderm can be seen. On following the mesoderm towards the dorsum, it becomes gradually thicker. In the mesoderm of this region there is found an extensive cavity (*cœl.*), which is usually irregular in outline, and might be mistaken for a *wholly* artificial condition. That the two layers were once in contact is shown by the correspondence of outline on the two sides of the space. The separation along this line is so regular, however, in successive sections, and recurs so frequently in other embryos, that the cavity must be regarded as an artificial expansion of an already existing split, rather than as an indifferent rupture of a solid mass of cells. In many sections of this embryo it is easy to trace a line of division reaching from the ventral cavity (cœlom) to the large lateral cavity just described. This, then, represents a portion of the cœlom (normally, I believe, closed), and the layers of mesoderm on the two sides of it are consequently somatopleure and splanchnopleure. The mesoderm in this region, as I have stated, is several cells deep. Along the inner and outer edges of the wedge-shaped plate of tissue constituting the mesoderm of either side, the cells, except where artificial ruptures occur, are in close contact, and form an epithelial lamella. The central portion of the plate, where this is more than two cells in thickness, contains cells of a more rounded shape, which do not form definite rows, but which are closely applied to the outer layer, — a condition which becomes quite evident when the cœlom is artificially enlarged.

The somatopleure of this region, then, is a layer at least two cells in thickness. The splanchnopleure, on the other hand, in this as in later stages, consists of a layer one cell in depth, extending from the ventral surface of the animal to the protovertebral plate.[1] Naturally no sharp line of division can be drawn at this stage between the protovertebral plates and the adjacent portions of the lateral plates. In the section under consideration, the protovertebral plate is rather compact, and it is difficult to indicate with certainty the boundary between the somatic and splanchnic layers. A study of this portion of the mesoderm, however, has convinced me that the cœlom (*cœl.'*) is already outlined, and lies in such a position as to leave only a single layer of cells dorsal to it, — a condition which is perfectly evident in later stages. It is indicated by such a distribution of pigment as is seen to the right in Figure 3.

On following the series of sections farther towards the head, a constriction of the mesoderm appears beneath the lateral margin of the medullary plate, and the open cœlom is continued into the protovertebral plate. In a section 1.2 mm. from the posterior end the somatic and splanchnic layers are each but one cell thick in the region of the protovertebral plate. The cells of the somatic layer, which in the protovertebral portion are of a high columnar form, become tile-like beneath the pronounced lateral thickening (compare Fig. 1, *cras. gn.*) of the medullary plate. The somatopleure immediately lateral to the medullary plate is rather thick, and becomes thinner both towards the median dorsal and median ventral lines. The regularity of the bounding walls of the body cavity in this region, and the occurrence of a space where no other signs of distortion are apparent, lead me to believe that the separation of the two layers of mesoderm is here perfectly normal, and not, as in more posterior regions, an artificial separation of two closely applied lamellæ.

It is, in general, very difficult to observe karyokinetic conditions in mesodermal or yolk cells, owing to the presence of the large and numerous yolk spherules ; but I am reasonably certain that I have observed cells in the somatopleural thickening, dividing in a plane parallel to the surface of the layer ; i. e. the cells were dividing in such wise as to increase the thickness of the layer.

In a section 1.32 mm. in front of the posterior end, the lateral portion of the medullary plate is greatly thickened, and the lateral plates are thereby wholly cut off from the protovertebral plate. The thickening of the medullary plate is the hinder portion of a considerable ganglionic mass, which is the basis for the subsequently differentiated ganglia Gasseri, acusticum, and nodosum.[1] The somatopleural thickening may be traced to a point about 80 μ farther forward, where the body cavity is no longer expanded. The relations of this thickening to the nephridial organs will be discussed in connection with Stage II. (page 211).

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[1] The differentiation of the protovertebræ has not yet begun in this region, and I shall designate the thick masses of mesoderm on each side of the chorda as protovertebral plates.

In a slightly older embryo, measuring 2.34 mm. in length, the condition of the mesoderm is nearly the same as in the one last described. The somatic layer shows a marked thickening (Plate I. Fig. 1, *cras. so'plu.*), which is greatest immediately lateral to the protovertebral plate. An anterior cœlomic chamber is also present. The anterior limit of the thickening is situated, as before, about 0.1 mm. in front of the hinder end of the enlargement which is destined to give rise to the cranial ganglia. The thickening (Fig. 1, *cras. so'plu.*) of the somatopleure is slightly more pronounced than in the younger embryo.

The results of this study may be summarized as follows. There exists already at this stage a slight somatopleural thickening, which is maximum along a line immediately lateral to the protovertebral plate. This thickening is associated with a local expansion of the cœlom. It is most pronounced in the region directly posterior to the cranial ganglionic mass. Posteriorly it is lost in a general lateral thickening of the somatic layer. The location of the thickening corresponds closely with the region in which the pronephros and segmental duct later arise. Whether we have in this thickening the first rudiment of the excretory system will be discussed in connection with Stage II.

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[1] I may here note that I have been able to make out for the series of spinal and cranial ganglia in Rana, Bufo, and Amblystoma an origin not unlike that described by Beard ('88, pp 166, 183) in Selachii and Aves, and by Schultze ('88, p. 349) in Rana. The ganglia are developed from the ectoderm at the lateral margins of the medullay plate (Fig. 3, *fnd. gn. spi.*). The differentiation of the ganglia is already apparent before the neural tube is infolded A spinal ganglion does not arise as an outgrowth from the neural tube, nor as a separate thickening of indifferent ectoderm, but is differentiated from a first rudiment (Anlage) common to it and to the neural tube.

Stage II.

Plate I. Figs. 4, 5. Plate II. Figs. 13, 14.

This stage includes embryos with a distinct medullary groove, the edges of which, however, have not yet fused to form a complete neural tube. Several protovertebræ can be distinguished.

In treating of the structure of the pronephros in this stage I shall first consider two embryos, which, judging from external appearances, seem to have reached the same stage of development. These embryos are about as far advanced as the one figured by Hertwig ('83, Taf. V. Fig. 6). In both the medullary groove is widely open. They are about 2.5 mm. long, and have been sectioned, one transversely, the other frontally.

Following the series of cross sections forward from the tail end, and comparing them with those of the preceding stage, the changes which have occurred will be apparent. In the posterior region, the mesoderm, as it passes outward and downward from the chorda, tapers much more rapidly than in the earlier stage. Even as far posteriorly as a few sections in front of the blastopore, this condition can be observed ; and, in a section 0.72 mm. from the posterior end, the thick central mass of mesoderm, the protovertebral region (Fig. 4, *la. pr'vr.*), has a triangular outline in cross section, and is readily distinguishable from the lateral plate (*la. l.*), with which it is continuous at its outer angle. The protovertebral plate consists of an outer epithelial layer and a central mass of cells. It is the former which is prolonged into the lateral plates. Each of these is here in general only one cell deep. Between somatopleure and splanchnopleure a few scattered cells occur, which can be assigned only with difficulty to either layer.

At 0.96 mm. from the posterior end the hindermost protovertebra visible in cross section can be distinguished. Between this point and the ganglion nodosum four protovertebræ are to be observed. Passing farther forward, it is difficult to assign boundaries to the protovertebræ. There is certainly one which is partially broken up into mesenchymatic tissue.[1] Still farther forward the series of the protovertebræ is continued by mesenchyme of a yet looser structure. Inasmuch as I have reached no conclusions respecting the number and position of the head somites, and since great diversity of opinion exists in the accounts to be found in the literature, I shall make no attempt to number the protovertebræ with which I shall have to do in any other way than by beginning with the most anterior that is readily distinguishable. Disregarding, then, the one which is wholly broken up into mesenchymatic tisue, somite I. lies in the same transverse plane as the fundament[1] of the ganglion nodosum, and extends backward to the hinder end of that structure. This protovertebra also shows signs of extensive conversion into mesenchyme, although part of it at a later stage undergoes muscular differentiation. Somite II. is the first of the series of well developed trunk protovertebræ. In the specimen under consideration somites I. to VI. are already differentiated.

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[1] I use this expression merely as descriptive of tissue of a certain histological character, quite independently of its origin. Indeed I am convinced, from observations which appear in the sequel, that not merely the head mesenchyme, but also much of that in the trunk, arises in relatively late stages from mesodermal tissue, substantially in accordance with the account of Balfour ('78, pp. 107 *et seq.*), which has recently found champions in Ziegler ('88) and others.

As I have stated, the somatopleure in the middle of the trunk consists of a layer one cell deep, to which a few loose cells lying between it and the splanchnopleure may possibly also be assigned. In the region of somite IV. the somatopleure becomes thickened. The thickening is greatest at the level of the lower margins of the protovertebræ (compare Plate II. Figs. 15, 16), and tapers both dorsally and ventrally. It is to be remarked in this connection that the protovertebræ are not yet fully separated from the lateral plates; but that in cross sections through the middle of a somite, — i. e. midway between the anterior and posterior faces of a protovertebra, — the cœlom can be traced to the dorsal margin of the protovertebra, and furthermore that the somatopleure and splanchnopleure are seen to be continuous with the somatic and splanchnic layers of the protovertebræ. The somatopleural proliferation extends forward as far as the anterior face of somite II. The cells in the thickening have a columnar shape, and are at least two deep. In some sections I have observed, in addition, a third row of thin cells next the body cavity. Near the ventral limit of the thickening a nearly horizontal line of division in the substance of the thickening can be observed. When seen in cross section, this line is slightly concave above. It is here that ruptures produced by artificial causes are likely to occur, and the line thus indicated marks, I believe, the lower limit of the pronephros. The somatopleural thickening is the fundament of the pronephros, and I shall call it in the following pages the

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[1] In the following pages I shall use the word *fundament* as an equivalent of the German expression *Anlage*, the term *fundamentum* having been adopted as the basis for the lettering of the figures of such structures in the "Contributions" from this Laboratory.

pronephric thickening. The dorsal portion of the expanded body cavity is the pronephric chamber.

The question whether the somatopleural thickening described in Stage I. be an early condition of the pronephric thickening is only to be answered by considering the fate of the former. Behind somite IV. this early thickening wholly disappears, and the one which is seen at a later stage is an independent formation. This conclusion is justified by a comparison of Figure 4 (Plate I.), showing the somatic layer to be only one cell thick in the posterior region of an embryo of the present stage, with Figure 3, which shows a two to three layered somatopleure (*so'plu.*) in a somewhat more anterior region of an embryo of the next younger stage. In the region of somites II., III., and IV., however, the somatopleure never wholly thins out; but the thickening is here moulded into a more definite form, and becomes the fundament of the pronephros. To my mind, it is as if the mesoderm, in the process of becoming thinner, was overtaken by the necessity of affording material for the formation of the pronephros and duct, and, as a matter of physiological economy, used for that purpose an accumulation of cells already present. Indeed, from the form of the thickening in anterior portions of the embryo, I am disposed to regard the differentiation of the pronephric thickening in this sense as having begun already in Stage I.

The corresponding series of frontal sections shows five well developed protovertebræ, representing somites I.–V. (Plate II. Figs. 13, 14). A mass of mesenchymatic tissue in front of somite I. is doubtless the remnant of the rudimentary anterior protovertebra observed in the series of cross sections, and behind somite V. the differentiation of a sixth is faintly indicated. Above the level of the lower border of the chorda the protovertebræ are sharply marked off from one another, and the somatic layer is relatively thin. Near their ventral margins, however, the successive protovertebræ are in close contact, and the somatic layer shows a pronounced lateral thickening (Fig. 13, *cras. pr'nph.*).

On passing ventrally to the region of the lateral plates, the interprotovertebral constrictions vanish. Since frontal sections, however, do not here cut the layer of mesoderm perpendicularly, certain sections in the series show a distinctly segmented splanchnic layer, while the somatic thickening in the same frontal plane is unsegmented. Farther ventral there are no traces of segmentation in either layer. Here the splanchnopleure (*spl'plu.*) uniformly consists of a single layer throughout its entire extent. The somatopleure facing the ganglion nodosum, and also that in the posterior region, is thin; but in the anterior portion of the trunk, immediately behind the ganglion nodosum, there is a marked thickening (*cras. pr'nph.*), which ends abruptly in front, but gradually thins out into indifferent somatopleure behind. This thickening is distinctly present through a length of 0.5 mm., which is slightly greater than the extent of protovertebræ II., III., and IV. Still farther ventrally, the antero-posterior extent of the thickening is much diminished, the reduction taking place from both ends, so that in passing ventrally the region in which the structure is last visible is situated approximately beneath protovertebra III.

Another pair of embryos, one of which was 2.5, the other 2.6 mm. in length, presented a condition of the pronephros somewhat more advanced than that just described (Plate I. Fig. 5). In these embryos the lips of the medullary fold in the most advanced region were in contact, but had not yet fused. The anterior limit of the pronephric thickening was the same in position as in the younger pair of embryos, lying near the middle of somite II. A study of the arrangement of the nuclei in this region made it evident that there were at this stage in general three layers in the thickening. The innermost of these is the thinnest, and is destined to become the peritoneal covering of the pronephros; the other two represent the two walls of the pronephric pouch, soon to be described. The pronephric thickening in the region of the anterior face of somite IV. is shown in Figure 5. The section gives a somewhat false impression as to the somatic layer of the protovertebra, unless the relation of the section to the successive somites be borne in mind. The considerable thickening which this layer apparently undergoes on passing into the protovertebra is due to the circumstance that the section here passes obliquely through a portion of the anterior wall of somite IV. Sections through the middle of a protovertebra show a gradual thinning of the somatic layer as far as the dorsal angle of the mesoderm (compare Plate II. Fig. 15, which is a cross section of the following stage), where this layer is almost pavement-like. The pronephric thickening extends rather farther posteriorly than in the former pair of embryos, and while it is manifestly difficult to set a limit to the structure, I am confident that the thickening extends into somite V. This posterior extension of the thickening is to be regarded as the fundament of the *pronephric*, or, according to the later nomenclature of Balfour, the *segmental duct*.

The corresponding series of frontal sections shows six well differentiated protovertebræ, representing somites I.–VI. The same group of cells which I interpreted before as the last remnant of a rudimentary anterior somite is still present, and a few more posterior protovertebræ are in process of formation. Frontal sections just ventral to the chorda are very instructive. By following through a series of these, an idea can be had of the successive changes which take place in passing from the protovertebræ to the lateral plates, — a region of prime importance for problems respecting the development of the urogenital organs. In sections approximately tangent to the chorda at its ventral border (compare Fig. 5), the plane of the section passes through the ventral floor of the protovertebra, and cuts the somatic mesoderm near the place where the protovertebra passes into the lateral plate. The body cavity is expanded in the anterior part of the trunk. The mass of tissue on the median side of the body cavity appears very broad, owing to the circumstance that the plane of the section, as before noted, lies in the floor of the protovertebra. The somatic layer is several cells thick, and very compact in structure, owing to the fact that the section passes through the dorsal margin of the pronephric thickening. In following the series of sections farther ventrally, the boundaries between the segmental constituents of the pronephric thickening become indistinct; and in a section 90 μ farther ventral they have wholly vanished. This section, however, still shows traces of segmentation in the splanchnic layer, which is here reduced in thickness, the plane of this section having passed ventral to the floor of the protovertebra. Still farther ventrally the segmentation of the splanchnopleure likewise vanishes, and finally the pronephric thickening gives place to undifferentiated somatopleure. I have looked in vain for prolongations of the body cavity into the pronephric mass at this stage. I believe that the pronephric thickening is to be regarded as a solid proliferation of the somatopleure, in which, however, the somatic layer of the protovertebræ takes some part.

STAGE III.

Plate I. Fig. 6. Plate II. Figs. 11, 12, 15-17.

In embryos of this stage the medullary canal is wholly closed, the fundaments of two pairs of gills are present, and the auditory vesicle consists of a shallow depression of the deep ectoderm.

The pronephric thickening has now begun to assume a more definite form, and during this stage becomes converted into a tubular organ. I shall first consider the structure as seen in a series of cross sections from an embryo measuring about 2.7 mm. in length. Figures 15 to 17 are from this series. The anterior end of the pronephric thickening is located in somite II. The plane of the section from which Figure 15 was drawn passes somewhat behind the middle of this somite, so as to show the location of the constriction between the protovertebræ and the lateral plates. In the middle of the somite, the arrangement of the cells composing the pronephric thickening appears to be that of a fold in which the layers are in close contact. The thickening is composed of three layers of cells, and it is possible to trace the somatic layer of the protovertebra into the outer layer of the thickening. The lateral indifferent somatopleure is continuous at the ventral border of the thickening with the inner or thin layer which lies next to the body cavity. Near the upper border of the thickening this inner layer appears to be folded abruptly on itself to form the middle layer of the thickening. The middle and outer layers are continuous with each other distally, i. e. ventrally.[1] This anterior knob of the pronephric thickening (Fig. 15, *fnd. nph'st.*^{1}) is the fundament of the first nephrostome, a later stage in the development of which is shown in Plate III. Fig. 18 (*nph'stm.*^{1}). In Figure 15 the three layers are indicated by the arrangement of the nuclei. Of these the two outer form the fundament of the first nephrostomal tubule. The innermost layer represents the underlying peritoneum. In the region between somites II. and III., it is impossible to distinguish definite layers in the thickening.

On entering somite III., the pronephric thickening has a far greater breadth, and it consists of three layers, the meaning of which is to be understood by a comparison with the condition in the region of the first nephrostome, just described.

In somite IV. (Fig. 16) a division of the thickening into a dorsal and ventral part is indicated, near the termination of the dotted line (*cras. pr'nph.*). The dorsal part is the fundament of the third nephrostome, and the ventral part represents the anterior portion of the segmental duct (more properly, common trunk, see page 228). The ventral portion of the thickening can be traced backwards from this point through a distance of about 0.37 mm. Figure 17 is drawn from a section through a region near the anterior boundary of somite VII., and shows

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[1] The correlative terms *distal* and *proximal* are so frequently employed by German writers as synonymous respectively with *posterior* and *anterior* that it seems advisable to allude to the fact that they are not used in the present paper in that sense, but invariably with their primitive signification; thus, the distal portion of a process is that part which is most remote from the point of attachment, whether the structure project anteriorly or posteriorly, medially or laterally, dorsally or ventrally.

the thickening (*cras. pr'nph.*) near its posterior termination. The mass is evidently a thickening *in situ* of the somatopleure. On either side of the fundament of the segmental duct the somatopleure is one cell thick, whereas in the fundament itself it is two or three cells in thickness. If the additional cells arose by a free backward growth from the anterior pronephric mass, we should expect to find them lying on the external face of a continuous somatopleural layer. But, as a matter of fact, no such continuous inner layer exists; on reaching the thickened region, the somatopleure merely becomes several cells in thickness, the outer cells presenting really a somewhat more compact condition and a more linear arrangement than the inner ones.

The constrictions between the protovertebræ and the lateral mesoderm can be distinctly made out only in intersegmental regions. As is shown in Figure 15, between somites II. and III. the level of the constriction is immediately dorsal to the nephrostomal portion of the pronephric mass. In the region between somites III. and IV. the division occurs at a corresponding position. This series of sections shows no sharp separation between protovertebral and lateral mesoderm posterior to somite IV., the protovertebral plate being here only partly broken up into successive metameric blocks, which do not as yet possess sharp ventral boundaries.

In frontal sections, the pronephric thickening shows a similar condition (compare Figs. 11–14) to that which obtains in the case of the embryo described under Stage II. (page 213), the most noticeable difference being an increase in the thickness of the pronephric mass. The longitudinal extent of the thickening corresponds approximately to that of five somites, though the posterior limit is of necessity somewhat uncertain. The posterior portion has every appearance of having arisen in the same way as the part lying beneath somites II., III., and IV. The latter, however, represents, as we have seen, the future pronephros; the former is the fundament of the segmental duct.

In an embryo slightly older than those last described, the evidences of an incipient canalization of the pronephric system are more pronounced. In the region of somites II.–IV., the two outer layers of the pronephric thickening are separated from the peritoneal layer by a distinct line of division. In the intersegmental regions, the outline of these two layers is that of an elongated ellipse, the nuclei being disposed, for the most part alternately, on either side of its major axis. The significance of this distribution becomes apparent on studying later stages, in which a lumen has appeared in the organ. It is then found that the lumen occupies the position of the major axis of the ellipse, and that the nuclei of the bounding cells lie close to the interior surface of the wall. If a tube so constituted be compressed laterally, so that the lumen wholly disappears, it is evident that the cells of the opposed walls would be likely to accommodate themselves to one another so as to present an alternate arrangement of their nuclei.

Opposite the middle of a somite, the relations are somewhat different. Here the two layers of what I shall hereafter call the pronephric pouch do not remain confluent at its dorsal extremity, but separate, the outer becoming continuous with the somatic layer of the protovertebra, the inner with the deepest layer of the thickening, and thus finally with the lateral somatopleure. In this region the body cavity can be seen to project for a short distance between the two layers of the pronephric pouch, as shown in Plate I. Fig. 6, *cœl.* This figure demonstrates very clearly the relations of the pouch to the lateral mesoderm and the overlying somites.

In the case of the younger set of embryos which have been considered in this stage, it will be remembered that the boundary between the lateral mesoderm and the protovertebræ was evident only in intersegmental regions. In the somewhat older individual now under consideration, the constrictions between these two portions of mesoderm have advanced into segmental regions as well; so that now, for the first time, the precise relations between the fundaments of the nephrostomes and the protovertebræ lying above them can be accurately determined. The last remnant of the communication between the protovertebral cavity and the body cavity I shall call the communicating canal, following in this the nomenclature of Renson ('83). The section shown in Figure 6 passes through this canal (*can. comn.*), and it is to be especially noted that the constriction between the somites and the lateral plates takes place dorsal to the region of communication between the pronephric system and the body cavity. Immediately dorsal to the pronephros, the somite sends out a lateral fold of the somatic layer, which is destined to form the capsule of the pronephros, to which I shall have occasion to refer in later stages.

In somite IV., the division of the pronephric mass into a dorsal and ventral part is faintly indicated, but the dorsal part shows no trace of the lumen which is destined to become the third nephrostome. In this embryo, the constrictions between the protovertebræ and lateral plate have advanced into more posterior regions. In somite V. the constriction occurs immediately dorsal to the fundament of the segmental duct, which, as I have shown, is continuous anteriorly with the ventral half of the thickening appearing in somite IV. A series of measurements from the dorsal median line shows that the ventral portion of the pronephric thickening remains at a nearly constant level, so that the protovertebræ must reach a somewhat more ventral position in the posterior region than in somites II.–IV.

Figure 11 (Plate II.) represents a frontal section through the dorsal part of the pronephric pouch in one of the oldest embryos of this stage. It shows the course of the earliest fundaments of the three tubules which emerge from the somatopleure beneath protovertebræ II., III., and IV. The most anterior outgrowth, arising in somite II., inclines outward and backward into the region of somite III.; the second outgrowth proceeds from its origin beneath protovertebra III. directly outward; and the third outgrowth inclines forward, so that its distal extremity also lies in the region of somite III. As the review of the previous stages has shown, these fundaments of the tubules have *not arisen as separate outgrowths* from the somatopleure, but have been differentiated from the originally continuous pronephric thickening, the three fundaments being confluent distally.

In this section the nuclei are abundant along a central band, but scarce or wholly absent in peripheral parts. This peculiar arrangement becomes intelligible when we consider that the plane of the section passes almost tangentially through the curved dorsal wall of the pouch. As we have seen in transverse sections, the nuclei lie close to the inner lumen of the pouch; it is therefore only in the deeper central parts of the section that they are encountered. In a section 0.03 mm. farther ventral (Fig. 12), the lumen of the pouch can be made out, though it is not conspicuous. It is difficult to say whether at this stage the lumen is continuous throughout the whole structure. In many embryos the evidence of such continuity seems indubitable; whereas in others, apparently quite as far advanced in other respects, the lumen seems to consist of unconnected portions. In some instances where no trace of a separation of the walls could be seen, a line of pigment indicated the position of the lumen. Occasionally I have met with a distinct prolongation of the body cavity into the prônephric mass. This condition has been most frequently encountered in the case of the fundament of the first tubule. I am not, however, inclined to place much weight on such observations as proving the claim that the lumen of the pronephros forms as an ingrowth of the cœlom proceeding from the nephrostomes and advancing into the duct.

On the contrary, the lumen is already potentially present, as shown by the arrangement of the nuclei before any actual separation of the walls occurs. I am of opinion that, in the cases referred to, the separation is largely artificial, and that the ruptures take place most frequently at the nephrostomes for the reason that the walls, which elsewhere form a closed ring, here have in cross section the form of a sharp re-entrant angle bordering on a large open space. It is evident that in the former region the walls would be less liable to be torn apart in the preparation of the material than in the latter. In general, however, it must be admitted that the development of the lumen, like that of the system as a whole, actually advances from anterior to posterior regions.

The fundaments of the three pronephric tubules shown in Figure 11 are not to be regarded as outgrowths from the somites. They are, it is true, very closely related to the segments in their arrangement, but, as transverse sections prove (Plate I. Fig. 6, and Plate II. Fig. 15), they lie wholly ventral to the lower boundaries of the protovertebræ. The frontal section figured (Fig. 12) was chosen for the reason that it was the one which indicated most precisely the course of the fundaments of the three tubules. The plane of the section is parallel to a tangent to the dorsal margin of the structure, and passes only a little below that margin, not through the nephrostomes. These begin in a more ventral unsegmented region.

In the oldest embryos of this stage, the fundament of the duct has developed very rapidly. Anteriorly, it has in cross section a distinctly elliptical outline, and its cells have, with reference to the major axis of the ellipse, the same arrangement that I have described for the intersegmental regions of the pronephric pouch. On following the structure backwards, this distribution becomes less and less obvious, until the cells seem to have no definite arrangement. In this region the fundament of the duct is in far more intimate union with the somatopleure than was the case in anterior somites. In the region of somite IX. the last trace of the structure is to be seen as a simple thickening of the somatopleure, similar in form to that described and figured in the youngest embryos of this stage (Fig. 17), for a region just back of somite VI. The region in which the duct is formed is throughout immediately ventral to the constriction separating the protovertebræ from the lateral plates.[1]

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[1] In sections from the posterior end of the embryo, it is necessary to guard against the false appearances which arise from the obliquity of the plane of the

The mode of development which I have described in the foregoing pages, taken in connection with frontal sections, which show that the pronephric thickening tapers gradually backwards into indifferent somatopleure, seems to me to be very strong evidence concerning the precise origin of the duct. I believe I am justified in concluding that *the segmental duct between somites V. and IX. arises in situ from a thickening of the somatopleure serially equivalent to that from which in the anterior region the pronephros is developed.* Indirect evidence which can be brought to bear on this question will be reserved for the fuller consideration which can be accorded it, in connection with the following stage (page 222).

STAGE IV.

Plate I. Figs. 8, 9. Plate III. Figs. 18-26. Plate IV. Figs. 29, 39. Plate V. Fig. 45.

I have placed in this stage embryos of frogs taken from five different killings. They all belong to the fourth day after fertilization, and aside from individual variation show an evident advance in organization on the preceding stage. In all a distinct differentiation of muscular tissue has begun, the auditory vesicle is wholly cut off from the epidermis, and the ventral sucking (or more properly sticking) disks are well developed. In the following description, I shall find it convenient to distinguish a younger and an older set of embryos. In the younger set the embryos are from 3¼ to 3½ mm. long; they have about 14 protovertebræ and the fundaments of 3 pairs of gills. The embryos of the older set are from 3½ to 3¾ mm. long; they possess about 17 protovertebræ and the fundaments of 4 pairs of gills.

All the embryos of this stage have the pronephric pouch in its typical form. A side view of this organ with the neighboring portion of the

section to the vertical axis of the protovertebra. Cross sections in this region frequently encounter two contiguous protovertebræ. If the plane of the section traverse the communicating canal of a protovertebra, it would also pass obliquely through the dorsal portion of the next anterior protovertebra. The latter would then appear in cross section as a distinct mass immediately lateral to the neural tube and the chorda, and would resemble the condition which a protovertebra presents when cut near its anterior or posterior wall. Immediately below this mass there would be found on the same cross section the ventral portion of the more posterior protovertebra, with the corresponding part of its cavity. The latter, however, being apparently a direct continuation of the body cavity, owing to the existence of the communicating canal, would appear to represent the dorsal part of the body cavity, and the fundament of the duct would thus seem to be farther removed from the dorsal angle of the body cavity than it really is.

segmental duct is shown in Figure 39 (Plate IV.). In this drawing, the outlines were obtained by reconstruction from a series of cross sections. The pronephric pouch is suspended from the dorsal angle of the body cavity by the nephrostomal funnels. Elsewhere it is wholly cut off from the mesoderm, and merely rests conformably on the outer surface of the somatopleure. The precise relations of the parts can be understood by referring to the series of cross sections shown in Figures 18 to 22 (Plate III.). Figure 18 represents a section through the left pronephros in the region of the first nephrostome. The location of the plane of this section in the reconstruction is indicated by the dotted line *18*, in Figure 39. The lateral plates are here wholly cut off from the protovertebræ, splanchnopleure and somatopleure being continuous with each other at the dorsal angle of the body cavity. Figure 19 shows the structure of the organ between the first and second nephrostomes. In this and the following sections it was found advisable to depict the pronephric structures of the *right* side in order to exhibit in each case the section which most clearly showed the structural conditions. The next drawing (Fig. 20) in the series represents a section through the second nephrostome. In the preceding section, — not figured, — the three portions into which the lumen is here divided are continuous. The constriction between the middle and the ventral lumen is artificial; for the cells occasioning this local closure do not belong to the proper wall of the pouch, but form a group within the cavity. In several instances I have observed such groups of cells lying entirely free in the lumen of the pouch (Plate V. Fig. 45). In the present case, however, the mass is very intimately connected with the adjoining walls. This condition is preserved through a distance corresponding to the thickness of two or three sections, but the mass terminates by becoming free from both walls, so that in cross section it has the appearance of an "island" of tissue occupying the lumen of the pocket. The occurrence of these islands within the cavity of the pouch is of significance in determining precisely how the organ is developed. It is difficult to comprehend how they could be formed, provided the canals were produced by a fold of the somatopleure. On the other hand, they are perfectly intelligible on the assumption that the canals arise by the rearrangement of a solid mass of cells into a peripheral layer with a central lumen. According to the latter view, the islands would represent residual portions of the pronephric thickening which had not been transformed into peripheral wall.

Returning now to the section last under consideration (Fig. 20), the ventral union of the walls of the pronephric cavity is, as I have shown, artificial; the constriction between the middle portion of the lumen and the dorsal, or nephrostomal, portion is more apparent than real, for it is formed by the posterior wall of the nephrostomal tube, the plane of the section not having cut exactly in the axis of the tubule. In the section following that shown in Figure 20, the pouch is detached from the peritoneum, and presents an appearance similar to that shown in Figure 19. Before the third nephrostome is reached, the canal is divided by a horizontal constriction into two tubes. The dorsal portion forms the tubule of the third nephrostome; the ventral portion is the anterior end of the segmental duct. Figure 21 shows these parts in the region of the third nephrostome. The section corresponds in position with the dotted line *21* in Figure 39.

In the following sections the duct rapidly assumes a more dorsal position (compare Fig. 39). It then proceeds directly backward, at the level of the constriction between protovertebræ and lateral plate. Figure 22 shows the duct in the region of somite VI. It has not yet been formed, however, throughout its entire length. On passing posteriorly, it gradually loses its lumen; then the circular arrangement of the nuclei indicating the position of the lumen also vanishes; the structure at length terminates as a simple thickening of somatopleure in the region of the tenth somite. In a few individuals, however, I found slight evidences of a mode of ending different from that just described. In one case the indications seemed so strong as to compel me to seek confirmation of the view that the duct takes its origin *in situ.* I shall therefore give the details of the evidence on this point, and discuss its probable significance.

Figure 23 represents in cross section the fundament of the duct in this specimen, as shown in the fifth section in front of its termination. The section of the mass here contains about eight cells, which are in close contact with the somatopleure. In the second section behind this one there are shown parts of four or five cells (Fig. 24). The protoplasmic patch in the centre (*cd.*) is wider than an average cell of the fundament, and probably represents the anterior ends of two cells lying in the following section (Fig. 25, *c.* and *d.*). Dorsal to this mass of protoplasm is a nucleated cell (*b.*), and above this a small area of protoplasm with a faint nucleus (*a.*) which is doubtless a portion of a cell the principal part of which was cut off by the preceding section. On the ventral side of the centre of the fundament there is also a round nucleated cell (*e.*). In the next following section (Fig. 25), there are two nucleated cells in the centre of the mass (*c.* and *d.*), which, as I have said, doubtless correspond to the central protoplasmic area (*cd.*) seen in the preceding section. The most prominent cells of that section are here represented by two faint circles of protoplasm (*b.* and *c.*). In the next following section, not figured, the duct terminates as a single non-nucleated mass, probably corresponding to the dorsal cell in Figure 25. This remnant lies in a distinct depression of the somatopleure (Fig. 26, *f.*). This depression continues backwards through the space of three sections. Instead, then, of terminating in a thickening of the somatopleure, the end of the duct lies in a groove of unmodified somatopleure. There is no tissue directly behind the duct for its further growth, and the inference is natural that the somatopleure is mechanically depressed before the growing tip of the duct. In fact, I believe this to be actually the case, and that in this region the duct does grow by a simple cell proliferation within its own mass.

The key to the situation is to be found in the location of the posterior end of the duct in this specimen. An enumeration of the somites shows that the sections figured lie at the hinder end of somite XI. To show the bearing of this fact, I shall anticipate some of the results of a study of Stage V. In a series of frontal sections of the latter stage, I have succeeded in locating with reference to the successive somites the position at which the duct opens into the cloaca. The openings are in the same vertical plane with the middle of somite XII. The posterior end of the duct, then, in the specimen which I have just described, is within the distance of half a somite from its final termination. In order to empty into the cloaca, the duct has to grow inward from its position at the lateral margins of the protovertebræ to a position much nearer the median plane. It is difficult to comprehend how the duct could make this extension, except by proliferation of its own cells. It is just in this region that I find evidences of such a mode of growth. If the inference I have drawn from the facts adduced be correct, it seems to me to add strength to the conclusion I have reached in regard to the general mode of formation of the duct, inasmuch as it has been shown to be possible to detect free growth where it exists.

That the duct arises in the way I have described, and is not developed from the ectoderm, is shown, moreover, by certain indirect evidence which may be properly discussed at this point. As I have already stated, the duct is developed in such intimate connection with the somatopleure that I have been led to believe that it arises throughout its entire length from a proliferation *in situ* of that layer. In almost all of my preparations the duct in its backward growth is separated by a considerable space from the ectoderm, and I have observed no instance in which it was impossible to distinguish a perfectly sharp line between the fundament of the duct and the overlying ectoderm.

In describing the germ layers in Stage I., I referred to certain histological criteria which might be employed in determining to which germ layer a given group of cells belonged. The most valuable of these is the difference in the size and abundance of the yolk spherules, which even in that early stage served to contrast sharply the mesoderm from the ectoderm. In later stages, this character is equally pronounced. When the duct appears, the cells which constitute it are not distinguishable in histological features from those of the adjacent mesoderm, but are very different from those of the neighboring ectoderm. It seems to me extremely improbable that the cells of the fundament of the duct, with their numerous large yolk spherules, should have been recently derived from those of the ectoderm, which are provided with only few spherules of much smaller size. It would be entirely contrary to our conceptions of the physiological nature of yolk, if in the course of embryonic development this material was increased instead of diminished in quantity.

A similar argument seems to me to afford evidence that the duct arises *in situ*. If the duct had grown freely backward from an anterior proliferation, such growth would in all probability have been associated with the consumption of yolk in the cells of the fundament, and the spherules would be smaller or less numerous than those of the adjacent mesodermal cells. This, however, is not the case.

I conclude, therefore, that the segmental duct arises throughout its entire length by a proliferation *in situ* of the somatopleure. Its posterior end, however, grows across to the cloaca free from adjacent tissue.

Returning to the pronephric pouch, I purpose describing the relations of that organ to the somites. The section represented in Figure 29 (Plate IV.) shows graphically these relations. The plane of section in this case was very nearly tangential to the somatopleure at the points where the nephrostomes emerge. In this section it is evident that the three nephrostomes lie precisely under the first, second, and third somites, behind the ganglion nodosum. These correspond to the somites which I have numbered II., III., and IV.; so that the pronephric pouch remains in the same position as the pronephric thickening of earlier stages. In Figure 21 (Plate III.) the last remnant of the canal connecting the body cavity with the cavity of the protovertebræ is faintly indicated (above the letters *cœl.''*) in the same transverse plane as the third nephrostome; and Figure 6, as we have seen, shows more plainly the same condition in the case of the second nephrostome at an earlier stage.

The structure of the protovertebræ in this stage (Plate V. Fig. 45) merits especial consideration. Already in younger stages there is a differentiation of a peripheral epithelial layer surrounding the dense central mass, or kernel of the protovertebra. Laterally this peripheral part is represented by the entire somatic layer, which is separated from the kernel by the protovertebral cavity (*cœl.*). Along the median and ventral boundaries of the somite, a layer having an epithelial character is also to be seen. Thus the central mass which is to develop into the myotome lies on the median side of the cœlom, and is wholly surrounded by an epithelial layer. Frontal sections show that this layer can be traced inward for some distance between successive somites, both from their median and lateral surfaces. Since the development of the protovertebræ proceeds from before backwards, a single frontal section shows successive stages in the changes which they undergo. From such a section it is apparent that neither the median nor the lateral portion of the peripheral layer develops muscular fibres. That portion of this layer, however, which is included between the kernels of successive protovertebræ, is apparently differentiated into muscle, and becomes merged in the myotomes. Very soon after the first development of muscle fibres in the myotomes, the peripheral portions which have not been converted into muscle separate from the central mass, and, while yet adhering in a lamella, show evident signs of disassociation. It is to be noted, that, in regions where traces of the communicating canal are still distinguishable, the median peripheral layer, not the kernel, is seen to be continuous with the splanchnopleure. The somatopleure, on the other hand, may be traced, as before, into the outer layer of the protovertebra. This peripheral layer I believe to be wholly converted, with the exception stated, into mesenchymatic tissue. In the stage before us we see that it is distinctly breaking away from the myotome, and that the cells are acquiring a flat tile-like form. In the following stage no layer that could properly be called epithelial is present. In its stead there is a considerable quantity of loose mesenchyme, and the lateral face of the myotome is covered by a sheath consisting of very delicate fibrillar connective tissue.

Not merely is mesenchyme produced by the thin peripheral layer of the protovertebræ, but in anterior regions considerable portions of the kernels of the protovertebræ also undergo a metamorphosis in this direction. Thus, if I be not mistaken, a protovertebra immediately in front of somite I. has been wholly converted into mesenchymatic tissue; the kernel of the succeeding protovertebra (somite I.) has given rise to a considerable quantity of mesenchyme; and the process has been manifested, though to a less degree, even in succeeding somites. Furthermore, having established the continuity of splanchnopleure and somatopleure with the median and lateral peripheral layers respectively of the protovertebræ, it seems to me the more probable that the former as well as the latter may give rise to mesenchyme. I have, in fact, seen conditions directly in front of the first nephrostome which indicated a very extensive production of mesenchyme from the lateral plate in that region.

My reason for dwelling at so great length on the derivatives of the peripheral layer of the protovertebra is, that this layer plays an important part in forming certain accessory portions of the pronephric system. I refer to the *capsule* of the pronephros. Already in the preceding stage I noted the occurrence of a lateral fold of the somatic layer immediately dorsal to the constriction between protovertebræ and lateral plates (Fig. 6). In the younger individuals of Stage IV. the fold covers the dorsal surface of the pronephric pouch, and extends a short distance down on its lateral surface (Figs. 18–21, *fnd. cps.*). In the older set of embryos it has reached the somatopleure ventral to the pronephros, and thus forms a complete investing capsule.

In frontal sections the fundament of the capsule may be seen to consist of a series of segmental outgrowths from the successive protovertebræ. Later, these segmentally arranged structures fuse into a continuous enveloping sheet.

Lateral to the pronephros the capsule presents in general a two-layered condition, the result of its having been formed as a fold; but on ascending to the level of the lower boundary of the somite, these two layers separate (Plate V. Fig. 45); one passes beneath the protovertebra, covering the pronephros on its dorsal aspect; the other is continuous with the somatic layer of the protovertebra, forming a lateral sheath to the myotome. These layers are present in the region both of the pronephros and of the duct, but are seen in their simplest condition in the region of the second nephrostome (Fig. 20); not merely because this is the middle of the pronephros, but also because the process is somewhat modified in the protovertebra next in front of it (somite II.). Somite II. is one of those in which a considerable portion of the kernel of the protovertebra is converted into mesenchyme. For this reason the inner layer of the capsular fold, after separating from the layer which forms the lateral sheath of the myotome, passes inward, and is there lost in a loose mass of tissue (Fig. 18), resulting from the disassociation of certain cells of the somite in that region. Intersegmental regions also present appearances which are confused by the occurrence of cells belonging to the partition between two successive somites. The points which I especially wish to emphasize in this description are (1) the origin of the capsule from the somatic layer of segmented mesoderm, and (2) the fact that the layer from which the capsule is developed is also in other regions converted into mesenchymatic tissue.

In the younger specimens of this stage a horizontal fold of the splanchnopleure is to be noticed, forming a slight ridge directly across the body cavity from the pronephros. It first appears in front of the second nephrostome, and develops from this point backwards. It is the fundament of the glomus or pronephric glomerulus.[1] In the earliest trace of this organ that I have been able to find (Plate I. Fig. 8) there were already a few small mesenchymatic cells (*ms'chy.*) located in the angle of the fold. The source of these cells I have been unable to determine with certainty. The nuclei of all the cells in the fold itself lie very close to the body cavity, and it does not seem probable that those small cells could be produced by delamination from the splanchnopleure without an actual migration of the nuclei of the somatopleural cells to the basal, or entodermal, surface of that layer. I have never seen signs of such migration, and I therefore do not believe that it occurs. Furthermore, the folded portion of the somatopleure does not at once become thinner than the neighboring portions of that layer. In older stages, such a thinning takes place, but it seems to be due to a superficial extension of the layer, rather than to delamination. The position of the nuclei of the large entodermal cells in this neighborhood is equally unfavorable for the formation of these small cells by delamination. The only remaining explanation is that the latter have migrated into their present position from relatively remote parts. Other loose cells may be found between entoderm and splanchnopleure, and the question here raised is only a part of the larger problem as to the source of all such cells, including those which bound the yolk veins. The fate of the cells which I have found in the fundament of the glomus, I shall consider in treating of a later stage. I may, however, here anticipate to the extent of stating that they are connective-tissue elements.

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[1] The former term seems to me preferable, and will be employed in the following pages. The exact relations of the glomus to the mesonephric glomeruli will be explained in the general discussion.

Figure 9 shows the fundament of the glomus in one of the older embryos of this stage. Within the hollow of the fold may be seen two cells (*ms'chy.*), which are to be regarded as the descendants of the first small cells to which I referred in the younger embryo. Their differentiation in the direction of connective tissue can be noticed throughout the whole extent of the fundament. The scattered rounded cells near them probably represent embryonic blood cells in the region of the aorta.

STAGE V.

Plate I. Fig. 10. Plate IV. Figs. 31-34, 40.

The embryos belonging to this stage are on an average about thirty hours older than those of Stage IV. At this period almost all of the eggs are hatched; and, the duct having opened into the cloaca, the pronephros becomes functional. The larvæ of this stage measure 5–7 mm. in length, the rapid increase in size being largely due to the growth of the tail.

The form which the pronephros presents in this stage has been studied by means of reconstructions in the case of four pronephridia. The diagrams on Plate IV., Figures 31 to 38, represent in a rough way the number and distribution of the convolutions which the tubules present in this and the following stage. Of these, Figures 31 to 34 relate to the present stage. Figure 40 is a more accurate view of the pronephros which I have diagrammatically represented in Figure 32. In Figure 40 the outlines were taken with but little modification from the original reconstruction. I have not hesitated, however, even in this case, to remove defects plainly due to artificial causes, such as distorted sections and inaccurate superposition.

Comparing this drawing with Figure 39, it is easy to follow the changes that have taken place. In the earlier stage the fundaments of the three tubules are already present. The first modification which may be noted is the deepening of the constrictions which are indicated between the successive nephrostomes. In this way are formed three transverse tubules, joining distally a longitudinal canal; the former are the nephrostomal tubules, the latter I shall call the *collecting trunk*. In this case the continuation of the collecting trunk pursues a nearly straight course to the posterior margin of the gland, where it emerges as the segmental duct.[1] A second change which is apparent in Figure 40

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[1] In Figure 40 the first nephrostomal tubule and the collecting trunk have a pink color, the second tubule is yellow, and the third is orange, whereas the segmental duct is uncolored.

is the growth of the collecting trunk in the region between the second and third nephrostomal tubules, and the consequent separation of the latter. The further complication in this case is mainly due to a convolution of the second tubule; slighter contortions occur in other parts. In the case of the pronephros diagrammatically represented in Figure 31, however, a canal, which corresponds to what we should regard in Figure 32 as the anterior portion of the segmental duct, has been folded first forwards, reaching nearly to the level of the first nephrostome, and then backwards. The bends which are convex anteriorly may be called the anterior bends; those which are convex posteriorly, the posterior bends. The universal occurrence of this condition in all older embryos makes it desirable to distinguish this bent portion of the tube and its derivatives both from the original longitudinal canal of the pronephros, which I have called the collecting trunk, and from the straight posterior portion, or segmental duct proper. In the following pages I shall speak of each *nephrostomal tubule* as extending from its origin in the nephrostome to its junction with the longitudinal canal, or collecting trunk. In the case of the first nephrostomal tubule, the point of union with the collecting trunk is usually marked by an abrupt change of direction; where this does not occur, however, the distinction between the two portions must be somewhat arbitrary. The *collecting trunk* forms the continuation of the first nephrostomal tubule, it receives in its backward course the second tubule, and may be regarded as terminating at the point of entrance of the third tubule. The *common trunk* arises from the point of junction of the third tubule with the collecting trunk, and, after making various convolutions, leaves the gland at its posterior end as the segmental duct. In the two pronephridia shown in Figures 31 and 33, we have before us examples respectively of the two principal forms of convolution which are to be recognized in subsequent stages, viz. the contortion of the second tubule and that of the common trunk. The third tubule finally undergoes convolution to some extent; but the first tubule and the collecting trunk take almost no part in the process. Although complication has appeared both in the second tubule and in the common trunk, it is to be noticed that these processes do not have a fixed sequence. I have numbered the diagrams on Plate IV. with reference to the state of development shown by the larvæ. In doing this, I have not been guided by the age alone, for the large amount of individual variation makes that method nearly valueless; but I have endeavored, by passing in review a large number of characters, to gain a notion of the relative degree of development shown by the larvæ.

The first of the series of diagrams (Fig. 31) shows complication to have taken place to a considerable extent in both the convoluted regions. In the next diagram (Fig. 32) the second tubule alone takes part in the complication. Figures 33 and 34 represent respectively the right and left pronephridia of one individual. In the right pronephros (Fig. 33) the typical condition of the common trunk is present, while the nephrostomal tubules have undergone no contortion. Likewise in the left pronephros (Fig. 34) it is the common trunk to which the increasing complication is due; but in this case there are two additional bends introduced by a slight folding backward of the middle of the anterior bend. The convolutions of the common trunk lie principally in the ventral portion of the gland. The tubes which in cross section are seen in the dorsal part are mainly the several nephrostomal tubules, and the collecting trunk. This condition is likewise retained in later stages.

The position of the pronephros with reference to the myotomes has not changed since the preceding stage. The whole structure is slightly longer, but the myotomes have also lengthened to the same extent. The three nephrostomes are situated, as before, beneath the first, second, and third myotomes posterior to the ganglion nodosum, and are segmental in position.

In all the embryos of this stage the duct has opened into the cloaca. It is to be remembered in this connection, that the morphological position of the duct is outside the somatopleure; so that the cœlom and two layers of mesoderm intervene between it and the intestine. As might be expected, the union does not take place until the segmented and unsegmented portions of the mesoderm have become separated from each other. The passage to the cloaca is then effected through the split thus produced, and consequently around the dorsal angle of the body cavity.

In the frog, there is a sharp histological contrast between ectoderm and entoderm, and there is therefore no difficulty in assigning a limit to the proctodæal invagination. The region into which the duct opens is the hind gut, and the intestine at this point is unquestionably lined with entodermal cells. The portion of the primitive gut posterior to the openings of the segmental duct forms the Amphibian cloaca, and corresponds precisely, I should say, with that part of the cloaca of Amniota which Gadow ('88, p. 28) has recently designated by the name *urodæum*. The wall of the intestine is not wholly passive in the union occurring between it and the duct. In front of the excretory openings, the lumen of the intestine has an elliptical form, its major axis being vertical.

On passing backwards, the dorsal half broadens and finally exhibits two lateral processes, or cornua, the walls of which are composed of a layer one cell deep. The ducts open into the distal ends of these cornua (see Fig. 27, showing the condition in Stage VI.). Behind the outlets of the segmental ducts, the lumen of the intestine has a nearly circular outline, and descends rapidly to the anus, or, as it may now more correctly be called, the cloacal aperture. I was able to see in Stage IV. faint traces of these intestinal cornua. The cells of the dorsal roof of the intestine showed in this region a looser structure, and a line of pigment indicated the region of the outfolding. The cells of the duct and those of the cloaca are histologically very different from each other, so that it is for a long time possible to draw a line sharply separating the two constituents where they have come in contact.

The pronephric system of tubules presents in this stage quite uniform histological characters. I shall therefore describe its typical condition, and then consider the modifications that are to be found in certain of its regions. The walls of the tubules are very thick, measuring on the average about 25 μ in thickness. They accommodate themselves readily to the structures with which they come in contact, becoming thinner opposite elevations in neighboring surfaces, and thicker next to sinuses. The size of the lumen varies greatly. In the segmental duct proper, the diameter of the lumen is about 25 μ; it is usually somewhat greater in the region of the convoluted tubules. The walls of the tubules are composed of an epithelium, consisting of a single layer of columnar cells. The radial dimension of the cells in the case of thick walls is approximately three times their width. Where the plane of the section cuts the wall of a tube tangentially, the cells may be seen to have a polygonal outline. The nuclei invariably occur close to the central lumen of the tube; each is large, and is usually provided with a single distinct nucleolus. The eccentric position of the nuclei is attended with a corresponding distribution of the cell protoplasm. By the picro-carmin method which I have employed, the yolk spherules take a bright yellow stain, and the nucleus a light red. The active protoplasm has a faint pink coloration, which, however, is wholly invisible if too much picric acid be left in the preparation. In young cells, where only a small amount of yolk has been consumed, the delicate tint of the protoplasm cannot be seen, since all the light passing through the section encounters yellow yolk spherules. As the consumption of the yolk progresses, the protoplasmic matrix comes into view. In the wall of the tubules, the yolk is crowded to the outer surface of the cell, and a sheet of protoplasm first becomes visible close to the lumen. It is here also that pigment makes its appearance.

The histological character of special regions now claims our attention. The pronephridia shown in Figures 31 to 33 are all histologically very similar, but in the case of the gland represented in Figure 34 some notable differences occur, which I shall consider later. The somatopleure covering the pronephros is at this stage very thin. Each of the cells composing the membrane is thickest in its central portion, and tapers rapidly towards its margins. In the more advanced larvæ, the cells have elongated to such an extent that the peripheral portion is reduced to a thin protoplasmic plate, which is nearly devoid of yolk spherules. The central mass, on the other hand, contains the nucleus, and nearly all the yolk spherules. The peritoneum is continuous with the columnar epithelium of the walls of the tubules at the outer rim of the nephrostomes, which have the characteristic form of a funnel. Before reaching the periphery of the funnel, however, the columnar layer becomes slightly thinner, and at the rim it tapers rapidly, until it becomes continuous with the peritoneum (compare Fig. 18 of a younger and Fig. 28 of an older stage). The nephrostomal funnels are always deeply pigmented. The pigment is most abundant along the incurved surface, but is quite dense even up to the rim. It continues for a variable distance into the tubules. In the case of the pronephros, represented in Figure 31, the whole system of tubes was pigmented from the nephrostomes to the posterior bend near the beginning of the common trunk. The pigment granules are always disposed in a layer along the free surface of the cells. The nephrostomal tubules show in general the typical character, which I have previously described. The collecting trunk appears to be quite rigid, for I have never seen such a reduction of its lumen due to pressure as other tubes exhibit. The calibre of this canal is usually larger than that of the nephrostomal tubules. The portion of the duct which lies behind the third nephrostome is nearly straight and of uniform calibre. Generally the lumen is slightly wider, and the wall thinner, than in the nephrostomal tubules. In the pronephridia, shown in Figures 31 and 33, the loop embracing the anterior bend of the common trunk seems to have but little rigidity. It follows a tortuous course, and frequently the walls are so closely pressed together that the lumen is locally obliterated.

A peculiar modification in the pronephros, represented in Figure 34, has been alluded to. In this case, the common trunk, after proceeding from the level of the third nephrostome for a certain distance forward along the ventral border of the gland, as in the other embryos, undergoes a change of structure at about the level of the second nephrostome. The lumen there begins to enlarge, and the wall to become thinner. Farther forward, the cavity of the tube becomes greatly dilated, and the bounding wall is reduced to a delicate pavement epithelium, having the same appearance as the peritoneum covering the pronephros. The tube again contracts shortly before attaining its most anterior bend. A similar dilation also occurs in the following stage, in the description of which I shall again refer to the chamber thus produced and suggest its possible function.

The pronephros at this stage is completely invested in a loosely fitting capsular membrane. The cells of which this envelope is composed have become very thin, so that they form a delicate sheet not more than 6 μ thick. The nuclei occur in slightly enlarged portions of the cells. They are rather small, and show a tendency to be flattened in the plane of the layer. At the lower outer angle of the myotome, the capsular membrane is continuous with the myotomal sheath, as in the earlier stage. The capsule covers the pronephros so loosely as to leave extensive spaces between the enveloping membrane and the tubules. These spaces, together with those between the convoluted tubes, form an extensive and complicated system of sinuses, which bound the pronephric tubules on every side (compare Fig. 28, belonging to the next older stage). Behind the last nephrostome, a considerable space intervenes between the wall of the capsule and that of the duct. There is thus formed a single continuous but irregular channel, which accompanies the duct throughout its entire course; it is also prolonged into the region of the gland as a large ventral sinus, which is triangular in cross section (compare the lower of the spaces marked *sn. sng.* in Fig. 28). This channel is the fundament of the posterior cardinal vein. The course of the vessel may be traced at this stage for a short distance behind the point where the ducts open into the cloaca. There are two veins connected with the anterior end of the pronephros. Of these the ventral one is the larger, and is continuous posteriorly with the cardinal vein. The dorsal vessel of the pronephros also unites with the cardinal vein by means of the spaces between the tubules. After passing forward and leaving the pronephros, the ventral vessel proceeds medianwards to empty into the sinus venosus, this vessel constituting the ductus Cuvieri. The dorsal vessel of the pronephros can be traced forward into the head. In the somite next in front of the first nephrostome, it lies between the ganglion nodosum and the myotome. It can be traced for some distance along the base of the cranium, passing close to the median wall of the auditory vesicle and the ball of the eye.[1]

There are two kinds of cells found within the capsule of the pronephros concerning which I have as yet said nothing. Those which are more numerous are scattered, of circular outline and of unform size. Each has in general three or four large yolk spherules, and the nuclei are rather smaller than in the cells of the tubules. Very similar elements abound in the fundaments of blood-vessels at this stage, and it is evident that the cells are embryonic blood corpuscles. The spaces in which they occur constitute a complicated system of communicating blood sinuses, and are continuous with the lumens of the vessels entering and leaving the pronephros.

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[1] In order to ascertain, if possible, what vein of the adult this vessel represents, it will be necessary to describe here its condition in later stages. In the oldest embryos I have examined, 8.5 mm. long, the vein runs forward from the pronephros parallel to the aortic root and its continuation, the carotid artery. The vein is separated from the arterial trunk by the ganglia nodosum and faciale. Recalling the earlier position of the vein, it will be seen that it has been transferred from the median to the external side of the vagus nerve. In an intermediate stage, I have been able to see the nerve during its transit through the vein, thus confirming an observation of Kastschenko ('87, pp. 275, 276).

Following the vein farther forward, it is found to pass immediately ventral to the auditory vesicle, directly in front of which it sends a branch around the ganglion faciale to the side of the cranium. Slightly farther forward the vein divides, its branches passing around the more anterior of two ventral processes of the ganglion faciale. The two trunks thus formed separate. One enters the orbit, and can be traced to the anterior end of the optic bulb. The other passes below the eye, and pursues a nearly straight course to the anterior horn lip.

A description of the venous system of the adult frog has been given by Gruby ('42) and by Ecker ('64–81). The distribution of the veins which enter the dorsal portion of the pronephros corresponds most closely with the internal jugular of these authors. From the figures of Goette ('75), however, there can be no doubt that the vein I have described corresponds to the one which he calls the external jugular. I have been able to find a vein entering the sinus venosus directly which agrees accurately with the inferior jugular of Goette, but I have found none corresponding to the one he calls the internal jugular. It is stated by Goette (pp. 759, 760) that the vein named by him external jugular receives large branches from the maxillary and mandibular regions. This character would seem to connect it with the external jugular of Gruby and Ecker. According to Goette (p. 765), however, the external jugular of Gruby and Ecker is the same as his inferior jugular. I believe this statement to be true, and it seems possible that Goette, who confesses that his studies upon the veins did not extend beyond the first larval periods, may have erred in his account of the distribution of these rudimentary vessels.

Since the preceding description was written, a paper by Marshall and Bles ('90^b) has appeared, which adds another to the divergent accounts I have reviewed. The inferior jugular of Marshall and Bles corresponds closely with the vein I have alluded to under that name. The anterior cardinal vein is described by these authors ('90^b, p. 236) as "formed by the union behind the ear of a jugular vein returning blood from the brain and dorsal part of the head, and a facial vein which lies superficially along the side of the head ventral to both eye and ear." These vessels are described in tadpoles, measuring 9 mm. in length. My own observations on larvæ of nearly this size do not agree with this description.

The other class of cells to which I have referred are mesenchymatic. I have carefully studied these cells in the endeavor to ascertain their precise origin. A mode of reasoning similar to that employed in discussing the probable origin of the inner cells of the glomus leads to the conclusion that the mesenchymatic cells of the pronephros cannot have been given off from the walls of the tubules. As I have stated, the cells in these walls are very thick, and their nuclei lie close to the lumen of the tube. Under these circumstances, it is difficult to understand how any cells of the tubule should divide so as to give off from their basal surfaces cells as small as those in question. The usual process of cell division, if it took place parallel to the surface of the layer, would result in the production of a small cell on the side toward the lumen and a large outer segment. Such a large cell might, it is true, by repeated divisions, break up into numerous small cells, but for several reasons I do not believe this to have been the case. If such a delamination and subsequent cell division took place, it would naturally be a conspicuous process; but I have never observed any evidences of it. This method of origin would involve a considerable thinning of the tubes, which does not take place.

There remain two other possible sources for the mesenchymatic cells of the pronephros. They may have arisen from the tissue bounding the pronephros, viz. the capsular membrane and the adjacent somatopleure, or they may have come from remote regions. In judging between these possibilities, it is important to consider the sudden appearance of the cells and the small amount of differentiation they have undergone. It seems to me highly improbable that they should have already accomplished any extensive migrations. Under these circumstances, such positive evidence as I am able to adduce is the more convincing. In studying the youngest stages in which mesenchyme was present in the pronephros, this tissue was usually found near the somatopleure or the capsule, and frequently consisted of a row of cells closely applied to one of these layers. Occasionally I have seen a layer of mesenchymatic cells arranged along the somatopleure in a very definite manner, so that the nuclei of the two layers lay directly opposite each other and the intercellular regions precisely corresponded. In such cases the evidence seems strongly in favor of delamination, but I have never seen a nucleus dividing in that direction. This negative evidence, however, should have little weight, since all cell divisions occupy a comparatively short time, and are also obscured by the numerous yolk spherules. The observations just recorded agree very well with the rapid thinning of the somatopleure to which I alluded in discussing the histology of the tubules. I conclude, then, that the mesenchymatic tissue of the pronephros arises from the adjacent somatopleure, and probably also to some extent from the capsular membrane.

The glomus (Plate I. Fig. 10) has attained in this stage nearly its final dimensions. The lateral plate having become wholly detached from the protovertebræ, the glomus has the appearance of being attached to the wall of the body cavity at its dorsal angle (compare Fig. 9, of a younger stage, and Fig. 47, of Bufo). There is some individual variation, but in general it may be stated that the ridge constituting the organ under consideration extends continuously from the first nephrostome backward to a position slightly behind the third. It appears in cross section (Fig. 10) obovate, being attached by the narrower end. In structure it is very compact, so that it is difficult to locate with precision cell boundaries in the dense interior mass. The investing portion consists of a single layer of cells, which is continuous with the peritoneum. These cells are large, and have the form of spheres flattened on their inner surfaces (compare Plate VI. Figs. 49 and 50, *la. pi'ton.*, which represent this layer in Bufo). They are slightly pigmented, and a distinct row of pigment granules can usually be seen close to the inner surface of the layer. These outer cells are evidently the representatives of the large cells of the splanchnopleure which was folded, at a previous stage (see page 227), to form the earliest fundament of the glomus (Fig. 9, *fnd. glm.*). In certain favorable regions I have seen a thin structureless membrane lying directly within the outer cellular layer (compare Figs. 49, 50, *mb. ba.*). When any of the cells of that layer become detached, which frequently happens, this basement membrane usually remains in place, and gives a sharp outer contour to the glomus in that region. Besides the compact mass of large cells there occur within the organ one or two cells in each section (compare Figs. 49, 50, *en'th.*) which have an elongated form. They lie close to the basement membrane, with which their long axes are parallel. In sections each cell has a central swollen portion containing the nucleus, from which it tapers in both directions. I have not been able to trace the delicate lateral portions to their terminations, but I believe that these cells form a complete endothelial lining, which follows closely the delicate basement membrane. They doubtless represent the loose cells alluded to in Stage IV. as occurring within the fundament of the glomus. Their origin I have already discussed in connection with that stage, where I showed that they were probably not derived from the outer layer of the glomus. Although the structure of the central mass of cells is, it must be admitted, somewhat obscure, I have found no evidences of the complication which Hoffmann ('86, p. 591) has recently maintained for it.

On the contrary, a comparison of many individual cells in this mass with the loose cells in the cavity of the aorta has made me confident that most of the cells contained in the glomus are embryonic blood corpuscles. It is possible, however, that others are derived from infolded portions of the outer layer of the glomus. They appear to have no representatives in early stages of the organ. In my opinion, then, the glomus is essentially a blood sinus, the wall of which projects into the body cavity, carrying before it the peritoneal layer.

The junction of the two aortic roots takes place very nearly opposite the first nephrostome (compare Plate IV. Fig. 28, *rx. ao.*). The aortic trunk thus formed (Fig. 10, *ao.*), since it occupies the space between the chorda and mesentery, passes close to the attachment of each glomus.

The precise relations of the aorta to the glomus are rather difficult to observe, since the former is peculiarly liable to injury in sectioning. The interior of the chorda at this stage consists of a frail vesicular tissue, whereas its outer sheath is tough, and resistant to cutting instruments. In sectioning, therefore, it collapses, and occasions serious distortion of the adjacent parts.

In the younger individuals of this stage, the cavity of the aorta did not seem to be sharply marked off from the root of the glomus; in several instances, indeed, I was able to observe a continuity between the endothelium of the aorta and that lining the glomus. In older individuals I have repeatedly noticed distinct branches from the aorta passing into the glomus (Plate I. Fig. 10, *va. sng.*). These observations were made, however, only on the most favorable sections, and I have been unable to ascertain the number or distribution of such branches. In both of the two most obvious cases, however, the vessel entered the hinder end of the glomus. Occasionally, the vessel to the glomus seems to be only a lateral branch given off from a vessel which can be traced between entoderm and splanchnopleure for some distance ventral to the glomus (Fig. 10, *va. sng.*, the lower of the two dotted lines).

I have spoken of the expanded dorsal portion of the body cavity, into which the nephrostomes open, and which contains the glomus. This portion of the body cavity constitutes the so-called pronephric chamber. It is not to be regarded as a closed cavity. Elsewhere the somatopleure and the splanchnopleure are closely applied to each other, but there is absolutely no fusion of these layers ventral to the pronephros.

Stage VI.

Plate III. Fig. 27. Plate IV, Figs. 28, 30, 35-38, 41. Plate VI. Fig. 51.

The larvæ included in this stage are in general two or three days older than those of the preceding stage. They are about 8 mm. long from the anterior end to the tip of the tail. In this stage, the body no longer tapers gradually from the branchial region to the posterior end; but a definite line of separation is established between the trunk and tail regions. In the tail a distinct membranous fin has appeared, both along the dorsal and the ventral median lines. The horn lips can be seen surrounding the mouth, and the external gills project prominently on both sides of the body.

The pronephros of this stage has developed along lines foreshadowed in the preceding stage. The general form of the organ can best be understood by reference to the series of diagrams (Figs. 35–37) and the reconstruction (Fig. 41) given on Plate IV. As will be evident at once, the gland has reached a high degree of complexity, produced, however, by a continuation of the same process of complication which had begun in Stage V. Thus the first nephrostomal tubule[1] and the collecting trunk retain throughout a nearly unmodified condition; the third nephrostomal tubule usually becomes slightly complicated; the second exhibits the greatest number of convolutions. The common trunk, however, is the part which has been principally concerned in producing the increased complexity of the gland. It is to be noted that this contortion is not of a wholly indefinite nature; indeed, there is considerable uniformity in the pronephridia of different individuals of the same stage of development. In Figure 31, representing a pronephros of a larva in Stage V., it is to be seen that there are only two bends in the common trunk, which extends forward to the anterior end of the gland. From this simple condition the later complications may be derived by a few simple steps. In order to follow the changes it will be advisable to

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[1] The same colors have been employed for corresponding parts in both Figures 40 and 41. Consult explanation of Figure 41.

distinguish: (1) posterior bend adjacent to the collecting trunk, (2) ascending arm, (3) anterior bend, and (4) the descending arm, which is continuous with the segmental duct. The simplest condition which I have found in Stage VI. is represented in Figure 35. This diagram relates to a larva of R. sylvatica Le C., and it is of interest to note its close similarity to Figure 38, which represents the pronephros of a larva of R. pipiens Schreb. (halecina) of this stage. These two pronephridia will be considered together. In both, the ascending arm of the common trunk makes either an S-shaped bend or a loop interpolated near the middle of its course; the transverse portion, or anterior bend, is thrown into one or two slight folds, and the descending arm shows two loops, one in the middle of the gland, and the other near its posterior end. The two remaining diagrams (Figs. 36, 37), though taken from different individuals, are alike in all essential particulars. The principal changes from the condition shown in the simpler pronephridia just described consist in the development of an additional loop in the course of the ascending limb, and of several slight folds in the transverse portion; the loops present in the younger individuals of this stage have persisted and become more extensive. In the case of the larva whose pronephros is represented in Figure 37, I made a comparative study of the pronephridia found on the two sides of the body. The comparison showed that a slight want of symmetry existed between the two sides. Occasionally the direction in which equivalent tubes were bent did not correspond. On the right side of the body (the one figured), for example, the hindermost loop of the descending arm was formed by an inward bend, while in the left pronephros the corresponding tube is bent outward. In the descending arm of the left pronephros a small loop occurs in addition to those present on the right, while one of the two loops occurring in the ascending portion of the right side is almost unrepresented on the left; thus, the right pronephros approximates in this respect the simpler organ represented in Figure 35. A more striking anomaly of the left pronephros consists in the occurrence of a slight bend of the collecting trunk between the junctions of the second and third nephrostomal tubules, so that the latter connects with an ascending portion of the collecting trunk. Finally, the third nephrostomal tubule of the left side joins the collecting trunk farther posteriorly than does the one on the right side. In general, however, it seems to me that the several pronephridia studied show a rather remarkable uniformity even in the details of the arrangement of their tubules.

The position of the pronephros with reference to the muscle plates is the same in this stage as in the foregoing. The lateral plate is now wholly cut off from the myotomes; but a study of serial sections shows that each nephrostome lies beneath a myotome. These myotomes correspond to somites II., III., and IV.

The course of the duct in this stage is the same as in Stage V. The openings into the cloaca (Plate III. Fig. 27, *dt. sg.*) are now situated at the bottom of a depression in the dorsal wall of the cloaca (*clc.*). While the excretory products enter the main cloacal chamber by a single aperture, a glance at the histological characters of the short median unpaired trunk shows that it is lined with entodermal cells, and is therefore really a diverticulum of the roof of the cloaca. The ducts of the two sides, therefore, are not to be regarded as uniting into a common trunk, but as opening separately into a dorsal diverticulum of the cloaca.

The histological characters of the pronephric system have not undergone any great changes since the preceding stage. Figure 28 (Plate IV.) shows a cross section of the left pronephros of the larva, whose right pronephros is diagrammatically represented in Figure 37. The plane of the section passes through the first nephrostome, and the transition from the pavement cells of the peritoneum to the columnar epithelium of the tubules is clearly shown. This section also shows, besides the first nephrostomal tubule, the anterior ends of two loops which belong to the transverse portion of the common trunk. The walls of all the tubules are thinner than in the preceding stage, and since the nuclei remain of about the same size as heretofore, they now occupy a far larger proportion of the cell, and in the case of the thinnest-walled tubules are frequently almost in contact with both the outer and inner surfaces of the cell. The amount of yolk in the cells is considerably lessened, especially in those parts which exhibit the greatest number of convolutions. In some cells, a single large spherule is the sole remnant of the formerly abundant yolk. Pigment is present as scattered grains in the walls of all the tubules; it also shows a tendency, as in the previous stage, to accumulate along the free surfaces of the cells. The nephrostomes, however, are densely pigmented on the surface that is directed towards the body cavity and the lumen of the tubule. The duct posterior to the pronephros (Fig. 30) offers no features worthy of special mention. It is accompanied throughout by the cardinal vein (*vn. crd.*), on the median side of which the earliest fundaments of the mesonephric tubules are visible.

I have described a special enlarged region of the convoluted duct in a larva of Stage V. A similar condition is apparent on both sides of the body in the case of the individual whose pronephros is represented in Figure 35. The dilated chamber (Plate VI. Fig. 51) is here formed by a great expansion of that portion of the ascending arm of the common trunk (*trn. com.*) which is adjacent to the collecting trunk (*trn. clg.*). A similar dilated chamber occurs in the pronephros represented in Figures 36 and 41 ; but in the latter case neither the dilation of the lumen nor the thinning of the wall is very pronounced. In both these cases the expanded chamber is present in portions of the tubular system which are exactly equivalent to each other. Under these circumstances, the expansion of the *descending* limb of the duct occurring in the pronephros of Stage V. (Fig. 34) seems quite anomalous. The dilated chamber is invariably, however, superficial in position, lying close to the capsular membrane. I have been unable to reach an entirely satisfactory opinion regarding its function. Since it is situated so near to the nephrostomes, it does not seem very well adapted to serve as a reservoir for the storage of fluids secreted by the gland, for by far the larger portion of the secreting surface is situated between it and the duct. However, the chamber doubtless receives whatever fluids are gathered by the nephrostomes or are secreted by the peritoneal tubules, and it is possible that the enlargement exists solely for this purpose. In following the duct from the dilated region towards its outlet, a greatly contracted portion is reached, and this may serve for the better retention of fluid contained in the chamber.

The capsule in these larvæ is not so well marked as in those of the preceding stage. Between the pronephric tubules and the ectoderm there has arisen a considerable quantity of mesenchyme, and the capsule now appears merely as the line along which this mesenchyme comes in contact with the pronephric tubes and blood sinuses.

In discussing the blood supply for the preceding stage, it seemed advisable to consider the vessels in older larvæ as well, and I shall therefore merely refer here to the account given in that connection.[1]

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[1] In all the larvæ of this stage which I have examined, I have observed a peculiar sac, of which I have been unable to find any mention in the literature. In the oldest larva of this stage it consists of a capacious sinus lying in the triangular area bounded by the myotomes, the somatic peritoneum, and the ectoderm. It extends backwards from the niveau of the third nephrostome for a length of two or three myotomes, and appears to be closed upon all sides. The sac lies in a mass of loose mesenchyme, but possesses firm walls, so that any opening would naturally be easily recognizable. In the interior of the sac, cells which are undistinguishable from blood corpuscles are found in considerable numbers. In a younger larva the sac occurs in a corresponding position, is nearly filled with blood cells, and is in open

The glomus is somewhat larger and more compact than in the preceding stage, and for that reason its structure is more obscure; but I have seen nothing which would lead me to believe that it differs materially from the condition exhibited by the younger glomi of Stage V. The organ is bounded by a definite peritoneal layer and contains blood cells together with embryonic connective-tissue stroma. The blood cells are usually contained in definite channels, and, being closely packed together, frequently appear in cross sections to be disposed with considerable regularity around a central point. This arrangement is naturally suggestive of a tubular or a rod-like structure; but the histological characters of the cells and the conditions exhibited by adjacent sections show that this impression is illusory. In short, I have been unable to find within the glomus any traces of the rods and thick-walled tubes which have been described by Hoffmann ('86, p. 591).

No closed pronephric chamber exists at this stage. In the most anterior sections in which the pronephric tubules appear, a blind anterior diverticulum of the body cavity is to be seen; but this unites with the general body cavity surrounding the intestine even before the niveau of the first nephrostome is passed. Throughout the remainder of the pronephric region the lung bud (Plate IV. Fig. 28, *fnd. pul.*) forms a ridge on the splanchnic side of the cœlom. This ridge partially separates the pronephric chamber from the general body cavity; and in the region of the third nephrostome a still more perfect closure is effected on the right side of the body by means of the approximation of a portion of the midgut to the peritoneum covering the pronephros.

Stage VII.

The age of the larvæ of this stage, reckoned from the time of fertilization, is about forty-seven days. A large gap therefore intervenes between Stages VI. and VII., and the older larvæ are studied merely for the purpose of observing the process of degeneration in the pronephros. In the larvæ of Stage VII. the mesonephros has already attained a degree of complication comparable to that gained by the pronephros at Stage VI., i. e. the same average number of tubes appear in cross sections through the two glands. The mass of contorted tubules in the case of the mesonephros, however, is formed wholly by the transverse tubules, while the

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communication with the cardinal vein. In a larva of intermediate age, the sinus communicates with the cardinal vein by means of a very narrow canal. Respecting the fate and the significance of this singular structure, I have no suggestions to offer.

duct pursues a direct course through the gland. The duct is situated in the dorsal portion of the mesonephros adjacent to the lower borders of the myotomes; its relations are therefore different from those of the longitudinal canal of the pronephros, since, as we have seen, the common trunk in the pronephros is greatly convoluted, and its windings occupy the ventral portions of the gland.

The marked signs of degeneration which the pronephros presents in this stage prevented my reconstructing the gland, since it proved to be impossible to follow any given tube throughout the entire series of sections. Indeed, I am convinced that the tubules are no longer strictly continuous. I must therefore content myself with a brief description of the histological features noticed.

The lumen of the tubules is greatly enlarged, and is frequently filled with a dense coagulum which stains similarly to protoplasm. The cell walls are very thin and show a tendency to become shredded or frayed along the interior surface. The membranes between the cells in the wall have become indistinct, and the number of nuclei in a given area is far less than in a corresponding portion of the wall in Stage VI. The nuclei are stained only feebly, but contain deeply staining granules, and seem to be disappearing, since one can observe numerous gradations between the typical nuclei and those which have become so pale as to be nearly invisible. The ground substance of the walls is slightly vacuolated and contains numerous scattered dark granules. Between this remnant of the cellular wall of the tube and the basement membrane, I have frequently seen small cells with deeply stained nuclei. These may possibly represent intrusive connective-tissue elements.

I regret that I have not been able to make an extended study of the degeneration of the pronephros; but the limit which I have set to my work is perhaps the least arbitrary which I could easily make.

B. Bufo.

The development of the pronephros and the segmental duct in Bufo is very similar to that which I have described for Rana. For this reason, I can treat the development in Bufo much more briefly, and shall lay principal stress upon those features which are unlike in the two genera.

STAGE I.

In the case of Rana, this stage included embryos which showed an ill defined somatopleural thickening lying immediately posterior to the cranial ganglionic mass. This proliferation proved, on comparison with older specimens, to be the first indication of the pronephric thickening. A similar condition of the somatopleure is presented by embryos of Bufo about 2 mm. long, in which the medullary folds are widely open.

The general relations of the germinal layers at this stage are almost identical with those in Rana, and the same histological criteria for distinguishing them can be employed. The ectoderm is very sharply marked off from the mesoderm. The former is deeply pigmented, while the adjacent mesoderm is almost destitute of pigment. The yolk spherules of the ectoderm measure on the average about 2 μ; those of the mesoderm, about 4 μ.

In embryos in which the medullary tube is still widely open, the somatopleure and splanchnopleure are separated from each other by a distinct space, the cœlom, which can be traced with perfect distinctness into the protovertebral plate, where it becomes slightly expanded. In the anterior half of the embryo, both the somatic and the splanchnic layers are only one cell in thickness. Posteriorly, and in the middle trunk region, however, certain loose cells bordering on the cœlom become associated with the somatic layer; but this layer is never, except at the extreme hinder end, more than two cells in thickness.

STAGE II.

Embryos in which the medullary tube is just closed exhibit a condition of the mesoderm slightly different from that of Stage I. In the posterior portion of the embryo, the mesoderm is quite thick in the region of the protovertebral plate, and becomes gradually thinner as it approaches the ventral portion of the body.

Anteriorly, the protovertebral plate shows traces of the differentiation of four or five protovertebræ. Of these, the most anterior lies in the same transverse plane as the ganglion nodosum, and, following the method of designation which was employed in the case of Rana, would properly represent somite I. This protovertebra, as in Rana, shows signs of transformation into mesenchyme, and is considerably compressed in the region of the ganglion.

The thickening has the general form which I have described for the corresponding stage of Rana, and its anterior margin is situated under somite II.

In the region of its greatest thickness, which is somewhat lateral to the boundary between the protovertebra and the lateral plate, it is two or three cells deep. It thins out slowly on the ventral side, much more rapidly on the side of the protovertebra, or dorsally. The thickening involves the ventral portion of the lateral wall of the protovertebra itself, although the greater part of the thickening is in the region of the lateral plate. I have not been able to find any sharp plane of division marking the lower limit of the thickening. The latter extends posteriorly through a distance of three or four somites, but it is difficult to make out its relations to the protovertebræ, in consequence of the small amount of differentiation which these exhibit at this stage. It seems to me, however, that the thickening reaches backward into a region posterior to that in which the pronephric tubules later develop, and therefore represents already the first fundament of both the pronephros and the anterior end of the segmental duct.

Frontal sections show the same relations between the pronephric thickening and the protovertebræ that I have described for Rana, but in Bufo the cœlom is entirely obliterated by the growth of the pronephric thickening, and consequently the pronephric chamber described in a corresponding stage of Rana does not exist in Bufo. This circumstance renders the determination of the precise boundaries between the two layers of mesoderm somewhat more difficult in the Toad than in the Frog, but still there is usually an unmistakable line of division between somatopleure and splanchnopleure even in the former. The pronephric thickening at this stage is from two to three cells thick, and is a solid mass.

Stage III.

In embryos of this stage, the fundament of a single pair of gill-folds is present; the fundament of the auditory vesicle consists of a simple thickening, which is just beginning to separate from the superficial ectoderm; and five or six protovertebræ have made their appearance. The embryos measure from 2.25 to 2.50 mm. in length.

The pronephric thickening becomes sharply marked off in this stage from the undifferentiated mesoderm lying ventral to it, and the canalization of the structure is accomplished by the arrangement of the cells around a lumen. Segmentally, the pronephric thickening has in general the form of a close fold of somatopleure, whereas intersegmentally it appears as a flattened tube. The points of continuity with the cœlom are situated each directly beneath the middle of a protovertebra, and the somites in which they appear are II., III., and IV.

The duct arises as a backward continuation of the pronephric thickening, and contrasts very sharply in histological characters with the ectoderm, in consequence of the pigmentation and paucity of yolk spherules in the latter.

STAGE IV.

Plate V. Fig. 43.

Embryos of this stage measure from 2.8 to 3.1 mm. in total length. Muscular fibres have begun to appear in the myotomes, the auditory vesicles are entirely detached from the external ectoderm, and the protovertebræ have been differentiated as far back as the anus.

The pronephric pouch of Bufo is very similar to that of Rana. It communicates with the cœlom by means of three nephrostomes, and from its ventral margin the duct takes its origin. The nephrostomes are segmental in position, and are situated beneath protovertebræ II., III., and IV.[1]

The duct can be followed for some distance posterior to the hindermost pronephric nephrostome as a distinct elliptical tube with a central lumen. The lumen, however, disappears further posteriorly, and the duct terminates either as a simple thickening of the somatopleure, or its posterior end merely rests upon the mesoderm in the region of somite XI. The hinder tip of the duct (Fig. 43, *fnd. dt. sg.*) in both cases resembles very closely the adjacent mesoderm both in the size and in the abundance of yolk spherules, and it differs from the ectoderm both in these features and in the scarcity of pigment. In Bufo I have never been so fortunate as to find the growing end of the duct situated in a groove of depressed mesoderm; but I believe that the fundament extends itself from the region of its origin in the somatopleure to the projecting cornu of the cloaca by means of an independent growth on the part of its own cells. The greater part of the duct, however, arises from a local proliferation of somatopleure.

The pronephric capsule in Bufo arises as a downgrowth from the outer peripheral layer of the protovertebræ. In this stage, however, it has not reached the somatopleure ventral to the pronephros, but merely forms a two-layered scale-like sheet of tissue covering the dorsal portion of the gland.

The pronephric chamber is present at this stage. The general body cavity, however, has not yet appeared, the somatopleure and splanchnopleure being in other regions in close contact.

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[1] I have preserved in the enumeration of the body somites of Bufo the same designations that were employed in the case of Rana. In Bufo, however, the kernel of the degenerate protovertebra in front of somite I. gives rise to a few muscle fibres.

STAGE V.

Plate V. Figs. 42, 46. Plate VI. Figs. 47, 49, 52.

At this stage the larvæ were hatched and swam about freely in the aquaria. The larvæ measured from 4 to 6 mm. in length, and each had a distinct tail, which protruded for a distance of 1.5 to 2 mm. behind the anus. The pronephros was probably already functional.

The character of the convolutions of the pronephric tubules was studied in the case of four pronephridia. In this feature one of them corresponded very closely with the condition in the pronephros of Rana represented in Figure 33. The remaining pronephridia differed from this type solely in the circumstance that the third nephrostomal tubule joined the collecting trunk at the extreme posterior portion of the bend, which in Rana usually forms the first portion of the common trunk.

The position of the pronephros with reference to the somites remains in general nearly the same as in the preceding stage. In individual cases, however, the nephrostomes do not appear to lie precisely under the middle of the myotome.

In embryos of this stage, the segmental ducts already open into the cloaca. These openings are situated beneath myotome XII. It is obvious from this fact that the duct in the older embryos of Stage IV. had already very nearly reached the region of its final communication with the cloaca. In Bufo the lumen of the gut is very narrow, and is separated from the lateral walls of the body by an extensive mass of yolk cells. The cloacal cornua are therefore in this case very long, extending to the outer surface of the entoderm. The ducts reach these cornua by passing between the dorsal angle of the body cavity and the overlying myotomes.

The histology of the pronephros in Bufo does not present any noteworthy features of difference from that in Rana. The tubes are all slightly smaller in Bufo, and their walls contain somewhat more pigment than do those of Rana.

The capsule envelops the pronephros and duct in the way that I have described for Rana, and it also encloses a series of blood sinuses which are developed from the posterior cardinal vein. I was not able to obtain in Bufo any additional evidence in regard to the origin of the mesenchyme of the pronephros.

Two veins emerge from the anterior end of the pronephros. One of these is the immediate continuation of the posterior cardinal vein, which, in passing forward as the ductus Cuvieri (Plate V. Fig. 42, *dt. Cuv.*), makes a rapid ventral descent to open into the sinus venosus. The other vein (Fig. 42, *vn. jgl.*) passes forward between the myotome and the vagus nerve. It evidently is one of the jugular veins, but I have not been able to study its distribution in later stages, and am therefore unable to state more precisely which vein of the adult it represents.

The structure of the glomus in Bufo is far more evident than in corresponding stages of Rana. In treating of the development of the glomus in the latter, I reached the conclusion that it arises as a simple fold of splanchnopleure, into which mesenchymatic cells migrate. In later stages I was able to identify the original outer sheath with a distinct basement membrane, and found within this membrane a large number of embryonic blood corpuscles, and occasionally certain cells which resembled in their histological characters those of the sheath or peritoneal layer. In Bufo the vascular system is less developed than in the corresponding stage of Rana; and, owing to the small number of the blood corpuscles, the remaining cellular elements come more plainly into view. The usual form of the glomus is that of a hollow peritoneal sac lined with endothelium (Plate VI. Figs. 47, 49, 50), and containing scattered blood corpuscles (Fig. 46). At the entrance to the sac the endothelium (*en'th.*) is continuous with the loose mesenchyme surrounding the aorta, and, in certain regions, the lumen of the latter can be traced into the interior of the glomus. This organ, then, exhibits markedly the character of a blood sinus, the walls of which project into the body cavity. Occasionally one encounters in Bufo certain minor pocketings of the peritoneal layer of the glomus, — invaginations into the lumen of the glomus at the place, e. g., occupied by the letters *cœl.''* (Fig. 52). If the cells at the apices of such invaginations were to become detached, this condition would serve to indicate the source of the pigmented cells found in the interior of the glomus in the case of Rana, although I have as yet reached no final conclusion in regard to this matter.

In this stage the body cavity exists as a distinct lumen only in the region from which the nephrostomes emerge, where it constitutes a pronephric chamber.

My studies on the development of the excretory organs in Bufo have not extended beyond the present stage.

C. Amblystoma.

Plate V. Fig. 44. Plate VI. Fig. 48. Plate VII. Figs. 53-56. Plate VIII. Figs. 57-65.

Amblystoma shows in the development of its excretory system many features of similarity to the Anuran forms already described. The differences, however, are far greater than those which exist between Rana and Bufo, and will require for their presentation a fuller treatment than was given in the case of the latter genus; but the development in all three genera is sufficiently similar to allow the recognition of the same successive stages, based upon the degree of complication exhibited by the pronephros.

STAGE I.

Plate VI. Fig. 48.

In embryos of this stage, the two lateral medullary folds have just fused to form the neural tube. The embryos have a slightly elongated form and measure about 3.7 mm. in length. They are slightly more advanced than the embryo of Amblystoma represented by Bambeke ('80, Planche XI. Fig. 35). The eggs from which I derived my series of embryos had been deposited for a variable length of time before they were collected, and I am unable to give the ages of the several stages.[1]

The general arrangement of the germ layers (Plate VI. Fig. 48) is similar to that which I have described for Rana and Bufo. The ectoderm (*ec'drm.*) consists in general of a single layer of cells, each of which has the form of a cube slightly flattened. Scattered ectodermal cells form an incomplete deep layer, which may gain in some regions, e. g. in the head, a very considerable development. The outer face of each ectodermal cell possesses a thin layer of pigment, but this is by no means so dense as in Rana and Bufo. At this stage yolk spherules are abundant in all the cells of the ectoderm.

The entoderm has nearly the same arrangement as in Rana, but the yolk cells are relatively more abundant, and the lumen of the gut is narrower. In the anterior region, the chorda consists of a simple fold in the dorsal roof of the intestine; but in the posterior portion of the body it is represented by a single row of high columnar cells, which form a layer convex from side to side towards the lumen of the intestine. This layer is the one which O. Hertwig ('83) has named the chorda-entoblast. The cells of the yolk entoderm are in general the largest in the body, and contain very large yolk spherules. The majority of the entodermal cells contain no conspicuous accumulations of pigment; but the latter may occasionally be found in considerable quantity, particularly in the cells bordering on the gut.

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[1] A quantity of the eggs of Amblystoma punctatum Linn. raised in the laboratory during the present season reached the several stages as follows: Stage I., 5 days; Stage II., 5 days, 12 hours; Stage III., 6 days, 15 hours; Stage IV., 7 days, 15 hours; Stage V., 8–14 days; Stage VI., 15–20 days. These figures are only approximate, and between Stages II. and V. the individual variation is frequently more than sufficient to cover the entire interval between two successive stages. The temperature of the water varied somewhat during the period, but I believe that 10 or 11° C. would be a fair average.

In the dorsal portion of the body, the mesoderm consists of two lateral masses of tissue, each of which spreads outward and ventralward from the neural tube, and joins its fellow of the opposite side in the ventral median line. Each of these masses of mesoderm is thickest next to the medullary tube, and gradually becomes thinner in passing outward around the mass of yolk cells. In the dorsal half of the body (Fig. 48) each mass of cells consists of two distinct layers, which are continuous with each other along the sides of the neural tube. They represent the first division into somatic (*la. so.*) and splanchnic (*la. spl.*) mesoderm, and the slight space which separates them is the cœlom (*cœl.*). On passing outward and ventrally, the two layers of mesoderm gradually approach, and at length are continuous with, each other; for a short distance farther, it is still possible to trace two rows of nuclei, indicating approximately the territory occupied by the layers; but this arrangement finally disappears, and before the ventral surface is reached the mesoderm has the form of a layer only one cell in thickness (*ms'drm.*).

In both somatic and splanchnic layers, the cells are of a nearly cubical form, but those of the parietal layer are rather thicker, and may be even columnar. The mesoderm of the ventral side of the body, on the other hand, is composed of more flattened elements. The cells of the mesoderm are in general intermediate in size between those of the ectoderm and of the entoderm. Their yolk spherules are much smaller than those in the entoderm, but resemble those in the ectoderm too closely to afford a thoroughly satisfactory criterion for distinguishing the two layers. The mesodermal yolk spherules are, however, *slightly* larger than those of the ectoderm; and in doubtful cases they may be taken into account.

The pigment of the mesoderm is usually collected along that surface of the cell which faces the cœlom, and may in part serve as a guide for following that cavity in cases where the bounding layers of mesoderm are in close contact with each other.

I have spoken of the somatic mesoderm as a layer a single cell in thickness; this is not, however, an adequate representation of the actual condition. In many sections there may be observed, from place to place, an additional cell associated with the otherwise single layer. The occurrence of an incomplete second layer of cells is most noticeable in the anterior portion of the trunk, in a region directly lateral to the protovertebral plate. It is probable that this slightly thickened somatic layer is the first indication of the pronephric thickening.

STAGE II.

Plate V. Fig. 44.

Embryos of this stage measure nearly 4 mm. in length; the medullary tube has become entirely separated from the superficial ectoderm, and three protovertebræ can be distinguished in longitudinal sections.

The fundament of the pronephros forms in this stage (Plate V. Fig. 44) an evident thickening of the somatic mesoderm lying immediately lateral to the protovertebral plate. Throughout the greater part of the thickening, the layer is obviously two cells thick, and occasionally three nuclei may be seen in a line perpendicular to its surface. The cells constituting the thickening are closely compacted, and do not appear to form definite layers. The fact that the thickening passes through a stage in which it is only two cells in thickness precludes the possibility of its being a disguised fold with closely applied walls, for in that event there must be at least three layers of cells involved. Neither the anterior nor the posterior limit of the thickening can be clearly determined at this stage. I am also unable to state definitely its relations to the protovertebræ, inasmuch as these cannot be adequately made out in transverse sections, and the extent of the thickening cannot be satisfactorily observed in such longitudinal sections as pass through both the protovertebræ and the pronephric thickening. The latter may be traced for a distance of about 0.5 or 0.6 mm. Each protovertebra at this stage measures about 0.27 mm. in length, so that the thickening extends through a length of about two protovertebræ.

In slightly older embryos the pronephric thickening becomes in general three cells in thickness; but it is still a solid proliferation, with no indication of extensions of the cœlom between the layers.

STAGE III.

Plate VII. Figs. 55, 56.

At this stage the young Amblystomas are about 4.3 mm. long and distinctly elongated in shape; but they show as yet no trace of a tail. They are further characterized by the possession of about eight well marked protovertebræ.

In all the embryos of this stage the pronephric thickening is at least three cells in depth, and has a definite ventral boundary. The thickening extends as far forward as the front face of somite III., and posteriorly tapers gradually into undifferentiated somatopleure. The backward prolongation of the thickening is the first fundament of the segmental duct, and may be traced at least as far back as somite VI. Both portions of the thickening appear to arise in the same way; namely, by cell proliferation in the somatopleure.

It is a matter of some difficulty to ascertain when the first trace of a lumen appears. Before the two walls actually separate, the nuclei frequently show an arrangement which is suggestive of an evagination; but one cannot always trust such appearances. Later, a line of pigment can be traced from the body cavity for some distance into the interior of the thickening, and finally the two walls separate, leaving a clearly defined lumen. In all cases, the two regions of continuity with the cœlom are opposite the middle of protovertebræ III. and IV. respectively; and there is no indication whatever of a continuous fold.

Although the pronephric mass thus shows evident signs of segmentation, yet, as is to be seen by a comparison of segmental and intersegmental regions (Plate VII. Figs. 55 and 56), the proliferation is not interrupted in the latter regions. In frontal sections through pronephridia in which a definite lumen has begun to appear (compare Plate VII. Fig. 55), there can be seen two narrow canals leading from the cavities of protovertebræ III. and IV. and extending outward as cœlomic diverticula into the pronephric mass. From this condition the hasty conclusion might be drawn that the narrow canals are in fact outgrowths from the *protovertebral* cavities. This however, in my opinion, is not the case. If the relations of the mesoderm in such a transverse section as is shown in Figure 55 be regarded, it will be seen that a frontal section through the pronephric region (in the figure cited, a horizontal section a little below the level of the letters *cœl.*′) would cut through the protovertebral cavity near its floor, and at the same time pass through the lumen of the pronephric thickening. Since, moreover, these two spaces are continuous by means of the communicating canal, it might at first appear that the latter belonged to the pronephric tubule. The fate of that portion of the tube, however, shows this interpretation to be incorrect, and that it was only by means of the communicating canal that the lumen of the pronephros communicated with the protovertebral cavity; for when the separation of the protovertebræ from the lateral plate takes place, the communicating canal, which is assumed to be the stalk of the pronephric diverticulum of the protovertebra, becomes closed, and the pronephros is thereby left in communication with the body cavity alone (compare Mollier, '90, Taf. XII. Figs. 10 *c.*, 10 *d.*, tr_1 and tr_2).

STAGE IV.

Larvæ of Amblystoma do not possess a conspicuous widely open pronephric pouch, such as has been described in Anuran species; but the proliferation becomes at once converted into a tubular organ. Indeed, the condition of the pronephric thickening in Stage III. is the one which is most similar to the Anuran pronephric pouch, since it is then a continuous structure having connections with the cœlom in segmental regions.

In slightly older embryos, the dorsal half of the pronephric thickening is no longer continuous through the region between protovertebræ III. and IV.; and from this region backward to the hinder face of protovertebra IV. the mass is distinctly divided into two tubes. Of these two tubes, the more median and dorsal is the second nephrostomal tubule; the more lateral and ventral is the common trunk. Finally, it is to be observed in a number of cases that an anterior loop of the common trunk occurs a short distance in front of the point of junction with the nephrostomal canals. The pronephros thus has a form which approximates very closely to the condition which forms the starting point for the next stage (Plate VIII. Fig. 58).

STAGE V.

Plate VIII. Figs. 57-60.

This stage includes embryos which have attained a length of from 5 to 6 mm. Many of the older embryos of the stage have already hatched; they possess well developed tails and swim about freely.

The general form of the pronephros has been studied by means of a number of rough reconstructions, some of which are represented by the diagrams on Plate VIII. In Figures 57 to 60 inclusive, which belong to this stage, no windings have been reproduced which were not of sufficient magnitude to form definite antero-posterior loops; and, further, in plotting these loops, no attempt has been made to preserve in the diagram the natural direction in which the tube is actually bent. However, the relative positions of the bends in an antero-posterior direction have been accurately reproduced.

In the younger individuals of this stage, the pronephros (Fig. 58) resembles in many respects that of Rana represented in Figure 33; but it differs from the latter, notably in the occurrence of two instead of three nephrostomes and nephrostomal canals. For this reason, there is no canal which corresponds to the collecting trunk of Anura, save that portion of the latter which intervenes between nephrostomes I. and II.; and in discussing the topographical relations of the tubules it will be needless to distinguish this remnant of the collecting trunk from the first nephrostomal tubule. In this simplest condition of the pronephros, the common trunk makes a single loop, the anterior curve of which is situated nearly as far forward as the level of the first nephrostome. In somewhat older pronephridia (Figs. 59, 60) the main bend of the common trunk occupies a position even in front of the first nephrostome, and a number of minor folds intervene between the junction of the nephrostomal canals and this most anterior fold. In none of the pronephridia of this stage is there any evidence of convolution in the nephrostomal canals.

One individual of this stage departed from the normal condition, in that it possessed three instead of two nephrostomal canals. This abnormality occurred on both sides of the body, and appears to be correlated with a less highly developed first nephrostomal tube. It is to be noted that the third tubule (Fig. 57) appears as an appendage attached to the most posterior loop of the common trunk. This topographical relation suggests that it is the most posterior of the three nephrostomal tubules which has been added to those normally present in Amblystoma, and this inference is shown to be correct by the relations which the several tubules bear to the body somites. The question whether the most posterior of the three tubules in this case represents the third nephrostomal tubule of the *Anuran* pronephros can be answered only by a consideration of the relations which the several nephrostomes in the two groups bear to the overlying protovertebræ, and will be recurred to in the general discussion which follows. I may here anticipate to the extent of stating that the first and second tubules of Amblystoma probably correspond respectively to the second and third of Rana and Bufo, the abnormal third tubule belonging to a yet more posterior metamere.

The position of the pronephric nephrostomes with reference to the myotomes was determined at an early stage by the location of the first metameric diverticula which are developed within the pronephric mass; and in the present stage these relations have not materially changed. The two nephrostomes of the normal pronephros lie beneath the third and fourth myotomes respectively. In the case of the pronephridia with a supernumerary nephrostome, the first two nephrostomes occur beneath myotomes III. and IV. respectively, while the third nephrostome is found beneath myotome V.[1]

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[1] Myotome I. of this enumeration reaches forward to the root of the vagus nerve, and is flanked on its outer face by a portion of the ganglion nodosum, exactly as in the case of the Anura described.

In this stage the segmental duct in the younger embryos shows somewhat different conditions from those found in the older embryos. In the case of unhatched embryos possessing the simple pronephros shown in Figure 58, the duct on passing backwards gradually diminishes in calibre, and finally loses all trace of a lumen. The fundament of the duct is in this region composed of four or five cells in each cross section, which are frequently arranged with some regularity about the centre as an axis. On proceeding to more posterior regions the fundament of the duct becomes intimately connected with the mesoderm, and is finally lost in that layer. In Amblystoma the histological characters of the mesoderm and the ectoderm are not sufficiently unlike to allow one to base on them a definite conclusion respecting the layer which has furnished the material for the fundament of the duct. In all cases which I have observed, however, the duct neither unites with the ectoderm nor terminates freely; but its posterior end invariably is closely applied to the mesoderm, and consequently is most probably derived from that layer. In view of the fact that the yolk spherules of the fundament of the duct are of the same size as those present in the adjacent mesoderm, I am of opinion that the duct has undergone no extensive independent growth, but has arisen *in situ* as a proliferation of the somatopleure.

In the older embryos of this stage, the duct has extended backwards to the region of the cloaca, and joins the latter near the posterior face of myotome XX. A distinct post-anal gut is present at this stage. Its anterior portion contains an evident lumen, and appears as a direct continuation of the pre-anal portion; its posterior tip is solid, and extends backward into the tail region for the distance of about one millimeter. From the ventral floor of this continuous intestinal tube, a median diverticulum leads backward and downward to the anus. The histological characters of this diverticulum differ markedly from those of the rest of the intestine, and by comparison with younger stages it becomes evident that the former has resulted from a proctodæal invagination. Where the intestinal tube is joined by the proctodæum the ventral portion, or cloaca, is T-shaped. The lateral arms receive the segmental ducts, and the ventral stem may be followed to the anus. In Amblystoma, then, the segmental ducts open into the intestine at the point where the proctodæal ectoderm and the entoderm pass over into each other. It is somewhat doubtful with which of the two germ layers the wall of the ducts becomes continuous; but it is possible that — in contrast to the condition obtaining in the Anura studied — the ducts open upon an ectodermal surface.

In the younger embryos of this stage, the walls of the pronephric tubules are all very thick; they gradually diminish in thickness as the embryo grows older. The lumen, on the other hand, is at first narrow, but afterwards becomes much wider. Its size varies greatly in different portions of the pronephros. For example, the lumen of the long arm of the common trunk, which forms the direct continuation of the segmental duct, is usually much narrower than the average lumen of the other pronephric tubules. The nephrostomal canals near their junction and the adjacent portion of the common trunk usually have a wide lumen. In the abnormal pronephros represented in Figure 57, however, the lumen of the first nephrostomal tubule was very narrow, a circumstance which, as I have already suggested, may possibly be correlated with the presence of a third nephrostome.

The lining epithelium of the tubes is composed of polygonal cells, which in the younger embryos have a high columnar form, but become gradually thinner as development proceeds. The nuclei when stained with Czokor's cochineal show a coarsely granular or reticulate structure, and are located close to the lumen of the tubule. The protoplasm takes a uniform delicate tint, which is masked, however, by the deeply staining yolk spherules. These are most abundant near the basal surface of the cell; they decrease in number and in size with the growth of the larva.

In the younger embryos of this stage, the somatopleure is composed of somewhat flattened cells, whose superficial dimension is approximately double the thickness of the cell. The walls of the pronephric tubules in these embryos have a thickness of about 37.5 μ, while the parietal peritoneum has an average thickness of only about 15 μ. These two epithelial layers are confluent at the nephrostomes, the wall of the tubule diminishing rapidly in thickness to that of the peritoneum. The nephrostomes, as well as many of the pronephric tubules, are slightly pigmented on their internal surfaces; but the pigmentation is by no means so conspicuous as in Rana and Bufo. In the older larvæ of this stage, the peritoneum is much thinner; but since the walls of the tubules have also diminished in thickness, nearly the same relations are to be observed at the nephrostome as in the younger embryos.

As in Rana and Bufo, the pronephric capsule in Amblystoma develops in the form of a downgrowth from the somatic layer of the protovertebræ. In Amblystoma the two-layered condition of the capsule and its connection with the overlying protovertebræ are maintained in the oldest larvæ of this stage. It seems probable, moreover, that the downgrowth from the protovertebræ is met by a more or less pronounced upgrowth from the somatopleure immediately ventral to the pronephros. The thickness of the capsular sheath gradually diminishes in the course of the development of the larvæ, but it is in general approximately equal to that of the peritoneum in the same individual. In the older larvæ, moreover, the pronephros, and especially the segmental duct, become partially covered by a downward extension of the myotome. In such larvæ the anterior limb bud is prominently developed at this stage, and its cells cover in part the posterior ventral portion of the pronephros.

The sinuses within the capsule are bounded by mesenchymatic cells and contain scattered blood corpuscles; they are continuous posteriorly with the posterior cardinal veins, so that the venous blood in passing forward from the hinder portions of the body bathes the pronephric tubules on every side.

The vessel emerging from the anterior end of the pronephros receives a large vessel from the head, and from the point of union the ductus Cuvieri leads to the sinus venosus. The former vessel is one of the jugular veins. The distribution of this vein and its probable representative in the adult will be considered in connection with the following stage.

The first trace of the glomus appears in embryos of this stage. It consists, as in Rana and Bufo (compare Plate I. Figs. 8, 9, and Plate VI. Fig. 47), of a horizontal fold of splanchnopleure lying close to the dorsal angle of the body cavity. This fold extends, when fully formed, from the first nephrostome backwards to the second. The outer layer of the organ consists, as shown by its development, of splanchnic peritoneum, which is usually bounded within by a sharp contour. I am of opinion that the latter is in reality a thin structureless basement membrane. The interior mass of the glomus consists of several different elements. In the young stages embryonic blood cells form a prominent constituent. Other cells are present, which have an elongated form and are evidently connective-tissue elements; and there appear to be still other cells which are of a less modified character and in which nuclear mitoses occur. Many of the latter may well represent young stages in the development of blood corpuscles, for I have observed mitotic division of blood cells even in certain older larvæ of Stage VI. In addition to the classes of cells just mentioned, there are a few large cells whose nature is to me quite obscure. These cells measure 60 μ or more in diameter, and contain large yolk spherules, which are closely packed together and make up almost the entire substance of the cell. The histological characters of these cells ally them most closely with those of the entoderm, and in the youngest stages in which I have been able to identify them they were closely associated with the yolk entoderm, which lies medio-ventral to the region of the glomus. It is probable that they arise from the entoderm and migrate into the interior of the splanchnopleural fold. I have been unable to find in either Rana or Bufo any cells similar to these large cells in the glomus of Amblystoma, and I have at present no suggestion to offer respecting their significance. The glomus, as I have already indicated, is a highly vascular organ, and even in the younger stages it is possible to find vessels which connect it with the aorta. These vessels usually follow the splanchnic layer quite closely, and appear to lie external to the large cells to which reference has been made.

In the younger larvæ of this stage the body cavity in the pronephric region has the form of separate chambers, from each of which a single nephrostomal tubule arises; but elsewhere the cavity is wanting on account of the contact of the peritoneal surfaces. In the older individuals it is expanded over a much larger area, but by the development of the lung bud a dorsal portion of the cavity is partially separated from the rest as a pronephric chamber.

STAGE VI.

Plate VII. Figs. 53, 54. Plate VIII. Figs. 61-65.

The larvæ included in this stage were taken from several different killings made in the course of three or four days. They measure about 9 mm. from the anterior end to the tip of the tail. An anterior limb bud is plainly visible upon surface view, and the tail is provided with a distinct membranous fin.

The great complication in the structure of the pronephros which is attained in this stage is accomplished by a continuation of the same process of forming convolutions that has been described for the preceding stage. Indeed, the separation of the two stages is at best quite arbitrary. Figures 61–65 represent various pronephridia of the present stage. It is to be noticed that the portion of the common trunk of which the segmental duct is the direct continuation can be traced from the anterior limit of the pronephros backwards without convolution, or after having formed a few insignificant loops. The common trunk from its junction with the nephrostomal tubules to this most anterior bend is thrown into a series of complicated convolutions, which may be so arranged as to present a gradation of considerable regularity (Fig. 62), or may be quite irregular (Fig. 65). In most cases, however, it is to be noticed that the arrangement of the loops is in general favorable for a compact disposition of the tubes (Fig. 62). The convolution in this stage is no longer confined to the common trunk, the nephrostomal tubules undergoing slight contortion (Figs. 63–65).

I have determined the positions of the pronephric structures to the somites in these later stages by their relations to the spinal ganglia. The first and second nephrostomes lie very nearly in the same transverse plane as the first and second spinal ganglia respectively. In the youngest larvæ of this stage the boundaries between the myotomes may still be made out in transverse sections, and the nephrostomes are then found to lie beneath myotomes III. and IV. It is probable that in later stages as well two myotomes occur in front of the first spinal ganglion.

The duct after leaving the pronephros pursues a nearly straight course backwards to the cloaca. In the larvæ of this stage, the post-anal gut has atrophied, and the ducts open into the intestinal tract just at the point where it bends downward toward the anus or cloacal aperture. The outlets of the two sides of the body are quite widely separated, never opening into an unpaired median depression in the dorsal roof of the cloaca, as is the case in the corresponding stage of Rana. The outlets of the segmental ducts are situated between the eighteenth and the nineteenth spinal ganglion, which would correspond to somite XX. or XXI. Their position is, then, the same as in the preceding stage. (Compare page 254.)

In the series of embryos included under Stage V., it was shown that the walls of the pronephric tubules became gradually thinner as the animal developed. In the pronephridia of the present stage the same process has been continued, and the cells are frequently so reduced in thickness that the nucleus appears to be in contact with the basal as well as the superficial, or inner, surface of the cell. Occasionally tubes occur whose walls are so thin that each nucleus causes a protuberance into the lumen of the tube. But wherever the thickness of the epithelium exceeds the diameter of the nucleus, it is to be noticed that the latter lies close to the inner surface of the tube, whereas the yolk spherules are accumulated in the basal portions of the cells. The yolk spherules are much less numerous than in the preceding stage. In many cells they are wholly wanting, and in all they now form a much less prominent constituent than the cell protoplasm.

The nephrostomes present no new features of interest in this stage. Most of the pronephric tubules contain more or less pigment, which is usually accumulated in irregularly distributed dark patches. In one or two instances I have had a fair degree of success in dissecting out the pronephros of a fresh specimen. In such an isolated pronephros the course of the tubes can be followed with tolerable accuracy in consequence of the pigmented areas occurring in their walls. The loss of yolk spherules, to which the pronephric tubes have been subjected on reaching the present stage, is shown in a striking manner by the transparency of the gland as contrasted with the snow-white yolk-entoderm.

The histological characters of the duct (Plate VII. Figs. 53, 54) resemble closely those of the pronephric tubules. Its calibre is greatest in the region immediately posterior to the pronephros (Plate VII. Fig. 54), becoming less as the duct passes posteriorly (Fig. 53). Throughout its course it is accompanied by the posterior cardinal vein (*vn. crd.*). In the older larvæ of this stage, the segmental duct in its passage backwards to the cloaca receives a large number of mesonephric tubules, which will be described in the sequel.

The pronephros of the present stage is covered on its dorsal surface by the main body of the myotomes. From the outer angle of each myotome, moreover, a distinct fibrillar sheet envelops the entire lateral surface of the gland. This layer is the capsule, whose origin has been discussed in connection with Stage V. In the present stage, it frequently becomes deeply pigmented.

The anterior portion of the pronephros is also overlaid by a stratum of smooth muscle fibres, which arises from the dorsal fascia. This muscular sheet is continuous in front with a muscle layer which is inserted upon the ventral surface of the mandible, and probably represents the depressor maxillæ of the adult.

The pronephros is also covered in part by the shoulder girdle, which in this stage is wholly composed of cartilage.

The vascular sinuses enclosed within the capsule are the direct continuations of the posterior cardinal vein. They also receive — usually about midway between the first and second nephrostomes — a blood-vessel, which may be traced nearly as far back as the cloaca, and which accompanies in its course the ramus lateralis of the vagus nerve (see Fig. 53, just median to *n. l.*). I am not aware of any prior mention of a vessel having this course, and am unable to state whether this vein has any representative in the adult.

The vessel emerging from the anterior end of the pronephros receives a vessel from the head, and the two form the ductus Cuvieri, which proceeds downward and inward to join the sinus venosus. The anterior branch may be traced forward into the head in the same direction as the original trunk ; it accompanies in its course the ramus lateralis vagi.

In consequence of the uncertainty as to what vein of the adult this vessel represents, I shall here digress to describe its distribution at this stage. For purposes of description, I shall follow it from its point of junction with the cardinal vein forward towards its finer branches. Before reaching the ganglion nodosum, it sends a branch dorsalward, which can be traced for a short distance between the lateral wall of the cranium and the ganglion. The main trunk continues forward external to the ganglion, and gives off a branch which passes around the posterior end of the auditory capsule and enters the cranium. The original vessel now passes forward through a narrow channel left between the auditory capsule and the articulating portion of the mandibular cartilage. Near the anterior end of the auditory capsule it divides into two branches, one of which passes dorsal to the eyeball, accompanying in its course the ophthalmic branch of the trigeminal nerve; the other branch passes ventral to the eyeball, and continues into the anterior maxillary region, following the course of the canalis nasalis. The main trunk runs nearly parallel to the aortic root and its prolongation, the carotid artery, the efferent branchial trunks joining the aortic root by passing immediately ventral to the vessel whose course I have been following. The vein evidently corresponds to the one described under Stage V. of Rana (page 233, foot-note), and appears to me to represent in all probability the internal jugular of Gruby ('42) and of Ecker ('64–'82).

The glomus is considerably broader and thicker than in Stage V.; but its longitudinal extent is about the same. In the middle of its course its distal edge reaches across the body cavity and fuses with the somatic peritoneum which covers the pronephros. The structure of the organ appears to be nearly the same as in the preceding stage, but the interior mass is so compact that one can distinguish little more than the nuclei, which present quite uniform characters. Cells which are unquestionably endothelial are frequently evident along the basal surface of the peritoneal layer; they also traverse the interior of the glomus dividing this space into compartments. Pigment is present both in the peritoneal wall and in the interior mass. It has a scattered distribution, appearing in the form of perfectly black patches. The large cells to which allusion was made in Stage V. are present also in this stage. They have about the same size and histological features that formerly characterized them. The pronephric chamber has not changed materially from the condition exhibited in Stage V. The most anterior pronephric tubules are situated immediately lateral to a diverticulum of the body cavity, which in sections through this region appears wholly isolated. On following the series of sections backward, however, the chamber enlarges greatly, even before the nephrostomes are reached, and is separated from the ventral portion of the body cavity only by the lung bud. Between the first and second nephrostomes, the pronephric chamber is divided into two parts by the fusion of the distal edge of the glomus with the somatic peritoneum covering the pronephros. Still farther posteriorly, an open communication is established, not merely between these two portions of the pronephric chamber, but also between the latter and the general body cavity.

In almost all the larvæ of this stage, the mesonephric tubules have appeared, and in many individuals they have already opened into the duct. There is always a space intervening between the pronephros and the mesonephros, in which no tubules are developed. This interval appears to be subject to some variation, but in the majority of cases it comprises four somites.

In the most anterior region of the mesonephros the tubules show traces of a metameric arrangement, but this is wholly lost in more posterior regions. These relations can perhaps be best illustrated by the accompanying table, which shows the positions of the right mesonephric tubules in the larva, whose pronephros is represented in Figure 64. The somites have been reckoned by reference to the spinal ganglia, but the results are here expressed in terms of the original metamerism of the myotomes.

Somite III. — Pronephric nephrostome I.
“ IV. — “ “ II.
“ V. — Tubules absent.
“ VI. — “ “
“ VII. — “ “
“ VIII. — “ “
“ IX. — 1 mesonephric tubule.
“ X. — 1 “ “
“ XI. — 1 “ “
“ XII. — 2 “ tubules.
“ XIII. — 3 “ “
“ XIV. — 3 “ “
“ XV. — 4 “ “
“ XVI. — 5 “ “

Each tubule of the mesonephros (Plate VII. Fig. 53) has the ordinary form, which has induced several authors to call it “sickle-shaped,” and consists of cells which are wholly devoid of yolk spherules, in which the nucleus occupies almost the entire body of the cell. Along the region which corresponds to the cutting edge of the sickle, a few loose cells (*fnd.*

glm.') occur, which constitute the earliest fundament of the glomerulus. The nephrostomes, however, have not opened at this stage.

In the region between pronephros and mesonephros (Plate VII. Fig. 54) certain masses of cells are found on the median side of the duct in the same position as that occupied in the posterior region by the mesonephric tubules. These cells do not form a continuous mass, but are interrupted at intervals. The cords of cells thus formed do not, however, appear to correspond in their arrangement to the metamerism of the body. It is possible that they represent rudimentary nephridial tubules, but the evidence in favor of this interpretation must be regarded as far from satisfactory.

I have been unable to ascertain the precise mode of origin of the mesonephric tubules, having sought in vain for nuclear mitoses which should throw light upon this question. There are in younger stages many retroperitoneal (subperitoneal) cells which might be collected and rearranged so as to produce the tubules; or, again, the fundaments of the tubules might be formed by proliferation from the peritoneum. The cells of the tubule have evidently undergone very rapid division, as is indicated by the complete consumption of the yolk; and this circumstance seems to me to favor the second view. Furthermore, I have found nuclear mitoses (Fig. 54) in the region immediately in front of the mesonephros which indicate that the cords of cells in this region arise from the peritoneum. Although I am unable to assert that the mesonephric tubules arise from the peritoneum, I am inclined to regard it as probable that they do. There is no evidence, however, of a definite invagination of the wall of the body cavity.

This is the oldest stage of Amblystoma which I have examined, and with it I close the descriptive part of this paper.

III. General Discussion.

Having presented in a purely descriptive manner the facts of development as yielded by my own studies, I shall now endeavor to use these observations as a basis for the criticism of the results of other investigators, and in closing shall point out certain general conclusions which seem to me warranted by such a review.

Recent researches have extended greatly the number of animals in which a homologue of the pronephros is known, so that it may now be fairly assumed that the organ appears in the ontogeny of all Vertebrates.

In view of much recent evidence (Hatschek, '88^{b}, Rabl, '88, Ayers, '90) which clearly supports the view that Amphioxus is closely related to Craniotes and occupies a position near the base of the Vertebrate phylum, the kidneys of this animal are of prime interest in the present connection. Notwithstanding the extreme importance of the subject, however, the relation of the excretory system of Amphioxus to other Chordates must still be regarded as a matter of considerable doubt.

At least seven different views have been advanced respecting the excretory organs of this animal. According to the earliest of these views, which originated with Joh. Müller ('42, p. 101, see also Langerhans, '76, p. 322, and Rolph, '76, p. 140), certain modified groups of cells lying in the posterior portion of the atrium are claimed to possess an excretory function. I presume that no morphologist would endeavor to homologize these excretory patches with the kidneys of Vertebrates. The same is true of the glandular structures described by Owen ('66, p. 533, Fig. 169, *h*), and the epithelial bands of Wilh. Müller ('75, p. 109). Nor can I see in the "pigmented canals," atrio-cœlomic funnels, of Lankester ('75, pp. 260, 261, and '89, pp. 394–397) any features which would definitely link them to Vertebrate nephridia.

The account given by Hatschek ('84) of his discovery of a single nephridium, which he believes to open into the pharyngeal cavity, is too brief to permit one to form a final judgment upon his interpretation. The observation has not been confirmed by any subsequent investigator save perhaps Lankester and Willey ('90, p. 459), who do not however regard this organ, which they call the sub-chordal tube, as a nephridium. There is nothing in its structure as described by either author which in my opinion justifies its comparison to a Vertebrate excretory tubule.

The most recent paper on this topic, which is by Weiss ('90), is of considerable interest from the physiological researches which it records: these show that a large portion of the atrial epithelium, as well as the excretory patches of Müller, have a well marked excretory function. Of greater morphological value is the description given by Weiss of certain small tubules in which the excretory function is peculiarly active. These tubules empty into the atrium at the upper margin of that cavity in the region of each secondary gill bar. They seem to project into the cœlom, but Weiss was unable to detect a continuity between their lumen and the cœlom. Since the relations of these tubules to the cœlom are not ascertained, I am of opinion that the observations of Weiss do not afford satisfactory reasons for regarding them as homologues of either the Vertebrate or the Annelidan nephridia. Weiss's account, however, is at least very suggestive. An important feature is the metamerism of the tubules; for while the metamerism of the gill bars does not correspond in the adult to that of the myotomes, yet we should not lose sight of the fact that according to Kowalewsky ('67, see his Figs. 36 and 39) such a correspondence exists in the embryo. At such a stage, then, there would be present a single excretory tubule for each myotome.

In a recent lecture before the Gesellschaft für Morphologie und Physiologie in München, Boveri ('90) has endeavored to show the existence in Amphioxus of homologues of the pronephros, the mesonephros, and the segmental duct. The tubules which Boveri regards as pronephric are probably the same structures as the excretory tubules of Weiss; and I infer that the same have been seen by Spengel ('90, p. 282), though this writer makes no suggestion as to their significance. Both Weiss and Boveri claim to have proved by feeding the animals with carmine that the tubes are actually excretory. According to Boveri, also, they open into the atrium at the upper margin of each secondary gill bar; but their course is somewhat differently described by the two authors. Boveri maintains that each tube communicates by means of several openings with the dorso-pharyngeal cœlom. As confirmatory of his position that these canals represent the pronephric tubules of Craniota, he describes the relations they bear to the gill vessels, which he identifies with the segmental vessels described by Paul Mayer ('87, p. 343) in Selachii. According to Rückert ('88, pp. 239–242), the glomus of Elasmobranchs consists of a rete mirabile in connection with these segmental vessels. Adjacent to the excretory tubules, Boveri finds that the gills display an increase in vascularity, and that anastomoses are formed between the branchial vessels. This condition does not seem to have been noticed by Weiss. Spengel, who made a special study of the gill vessels, describes a longitudinal vessel at a corresponding level (longitudinal trunk of the ligamentum denticulatum), but does not discuss its significance. It seems to me that Boveri's observations, provided they be confirmed, afford fairly satisfactory evidence of the existence of true nephridia in Amphioxus; and, as I shall endeavor to show in the sequel, that these are constructed on a type which may be assumed to represent a primitive condition of the Vertebrate kidney.

The starting point of Boveri's researches was the hypothesis that the atrial cavity and gonadial pouches of Amphioxus correspond to the segmental duct and mesonephros respectively of Craniota. The attempts of Haeckel ('74^a, p. 37, and '74^b, p. 305) and of Huxley ('76, pp. 221, 222) to discover a homologue of the segmental duct in Amphioxus must, in my opinion, be held to have at present merely an historical interest;

it remains for me to consider whether the theory of Boveri be better grounded.

The arguments which are adduced in favor of the homology of the gonadial pouches and the mesonephros may be reduced to the following points of similarity. The gonadial pouches of Amphioxus are metameric diverticula of the dorso-pharyngeal cœlom, in accordance with the established views of Kowalewsky and Rolph, as confirmed by Boveri, who finds in the adult a continuity of the epithelia belonging to the two tracts; the mesonephric tubules likewise are primitively metameric diverticula from the dorsal portion of the body cavity (see Sedgwick, '80[a], *et al.*). The generative cells develop in the walls of the gonadial diverticula; the early occurrence of germinal cells at the proximal ends of the forming mesonephric tubes has also been described by Rückert ('88, p. 257) for Selachii. Finally, the canal by which the gonadial pouches primitively communicated with the cœlom arches over the dorsal angle of the atrial cavity in a way that is very similar to that in which the mesonephric tubules curve outward to join the duct. The only reason — save those that require the prior assumption that the gonadia represent mesonephric tubules — which I can see for identifying the atrium with the segmental duct is the fact that nephridial (pronephric?) tubes open into it. This argument seems to me of very little weight. Boveri himself believes that the pronephros primitively opened directly to the exterior. Unless other evidence can be adduced, I see no adequate reason for regarding the formation of the atrial cavity as a step in the development of the segmental duct. On the other hand, that interpretation seems to me quite opposed to all that is known of the development of the segmental duct. As I have shown in the preceding pages, there can be no doubt that, in Amphibia at least, the duct develops solely from the mesoderm. According to the opposed view — the ectodermal origin of the duct — the development always proceeds from a *pair* of narrow rod-like thickenings of ectoderm, one on each side of the body, which are very different from the *unpaired* ventral groove from which, according to the most recent account (Lankester and Willey, '90) the atrium develops. If, now, we deny the homology of the atrium with the segmental duct, the outward arching of the gonadia becomes a most insignificant topographical resemblance. It seems to me that it would be manifestly unfair to base so far reaching a homology on the remaining points of resemblance, viz. the early occurrence of germinal cells in the mesonephric tubules, and the circumstance that the gonadia are metameric diverticula of the dorso-pharyngeal cœlom.

Turning now to Craniota, the pronephros in Amniota and Selachii is a wholly degenerate structure; in many Anamnia, however, it serves for a longer or shorter time as a functional excretory organ.

The pronephros of Dipnoi alone is wholly unknown. Beard ('90, p. 157) speaks of the transformation of a part of the pronephros into the Müllerian duct as "a well known fact"; but the only authority he cites in this connection (Parker, '89) does not make such a statement, nor have I succeeded in finding anywhere in the literature any account of the pronephros of Dipnoi. Unless Beard has personal observations on this matter, I believe that in Dipnoi absolutely nothing is known of the pronephros or its transformation, save such inferences as may be drawn from the adult anatomy. I shall therefore merely repeat the statement of Ayers ('85, p. 506), that the development probably proceeds as in Amphibia, since the adult urogenital system in this group presents the closest analogy with that of the Dipnoi.

The excretory system of Cyclostomes is similar to that of Amphibia. In Petromyzon a pronephros develops in the Ammocœtes larva, but aborts in the adult. The number of nephrostomes and of tubules is small (4, according to Wilh. Müller; 4 to 5, Shipley; 3, Kupffer; according to Semon, an inner and an outer row of nephrostomes are to be distinguished); and they communicate with an anterior expanded portion of the body cavity. According to Fürbringer ('78^a, p. 42), the pronephros extends over about four somites. Opposite the nephrostomes, a vascular organ projects from the root of the mesentery into the body cavity. This is the so-called glomerulus; as figured by Scott ('81, Taf. IX. Fig. 24), it strikingly resembles the glomus of Amphibia. According to Scott, the pronephric tubules develop secondarily as outgrowths from the segmental duct. On the other hand, Shipley has confirmed the statements of Müller and Fürbringer, according to which the nephrostomes and tubules are formed by the incomplete closure of a longitudinal groove of somatopleure. Finally, Kupffer maintains that the tubules arise as *three separate evaginations of the somatopleure*, a result which is in harmony with my own observations on Amphibia.[1]

In Myxine nothing is known of the early development; but in late stages an organ has been made known by the studies of Wilh. Müller

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[1] In Goette's ('88, p. 163) preliminary account of the development of Petromyzon he states that a pronephros develops in the *same* manner as in Amphibia. This would indeed be a conclusion acceptable to me, but until the accounts are more at one in regard to the latter group the statement is somewhat vague. I await with interest the publication of that portion of Goette's final paper which relates to the excretory system.

('75) and of Fürbringer ('78^a, pp. 38, 39), which plainly represents the Amphibian pronephros. Whether it ever persists in the adult is still a matter of doubt (see Weldon, '84); but in young individuals, at least, the segmental duct (ureter) is prolonged anteriorly to the heart region. Here it gives off numerous coiled tubes, which branch and open by funnel-shaped nephrostomes into the pericardial cavity. On its dorsal side, the duct gives off a few tubules which terminate in glomeruli resembling those of the mesonephros. This condition and the large number of tubules constitute the main points of difference between the Amphibian pronephros and that of Myxine.

The pronephros of Teleosts and Ganoids appears to me to be reducible to a single type of structure, which can be easily derived from the condition present in Amphibia and Cyclostomes (and Dipnoi?). The so-called head-kidney of Teleosts described by Hyrtl ('51, p. 29) is probably derived from the embryonic pronephros, though mesonephric elements may also be found in the adult head-kidney (see Emery, '82, p. 46).

According to Rosenberg ('67, pp. 42 *et seq.*) and Oellacher ('73, pp. 97–100), the excretory organs arise as a pair of grooves of the somatopleure directly beneath the protovertebræ. A process of constriction, which proceeds from a middle region forwards and backwards, leads to the conversion of each groove into a tube, the segmental duct. The anterior portion becomes wholly cut off from the body cavity, and is thrown into numerous coils. The tip becomes considerably swollen, and is invaginated by an outgrowth from the aorta forming a single glomerulus on each side.

Goette's ('75, pp. 826, 827) account of the development of the pronephric glomerulus in Teleosts is somewhat different, and affords a better basis for homologizing the pronephros of Teleosts with that of Amphibia. Goette maintains that the somatopleural groove is imperfectly closed in front, leaving a single nephrostome, opposite which a glomerulus (glomus) is developed. Subsequently, the pronephric chamber becomes separated from the rest of the body cavity, and comes to resemble a Malpighian capsule with its contained glomerulus. While Fürbringer ('78^a) confirms Goette's view, Hoffmann ('86, p. 621 *et seq.*) has quite recently reasserted that this Malpighian capsule is the blind infolded end of the segmental duct, and the homology with the Amphibian glomus and pronephric chamber, which appears to me probable, he denies. Hoffmann's position does not seem to me tenable in the light of comparative studies. Even though it should be shown that the ducts have absolutely no connection with the body cavity at the time when the glomerulus is formed, I could nevertheless defend my position by the assumption that the blind anterior end of the duct is a compound structure, representing both nephrostomal canal and pronephric chamber. It seems to me that, were it necessary to make this assumption, an extensive comparative study would justify such an interpretation.

The pronephros of Teleosts was long supposed to remain functional in the adult; but recent investigations seem to favor the conclusion that it never persists in fully mature individuals, with the possible exception of a few degenerate animals like Fierasfer (cf. Balfour, 81^b, '82; Grosglik, '85 and '86; Emery, '80, '81, and '85; Calderwood, '91).

The account given by Balfour and Parker ('82, pp. 415–424) of the development of the pronephros in Lepidosteus is in very close agreement with the development in Teleosts as described by Goette and by Fürbringer. The only conspicuous point of difference is, that, while in Teleosts the pronephric chamber becomes wholly detached from the body cavity, in Lepidosteus a remnant of the original communication probably persists as a so-called peritoneal tubule. As among Teleosts, the pronephros atrophies in adult Lepidostei.

Beard's ('89, pp. 114, 115) account of the early development differs greatly from that just given. According to this author, the pronephros is formed as a solid proliferation from the intermediate cell layer (Balfour) in the region from the 4th to the 8th or 9th somite inclusive. Externally, the proliferation fuses with the ectoderm. As a rule, there are formed three pairs of pronephric nephrostomes, of which the most posterior pair abort. The pronephric chamber is formed by the narrowing of the ciliated opening and the widening of the part opposite the glomerulus. Since Beard does not describe the development of the glomerulus, the account seems to me decidedly vague; but I believe I am right in accrediting to the author the view held by Hoffmann for Teleosts, that the glomerulus is not developed in the body cavity. As I understand him, it is developed in the course of the pronephric tubes.

All the studies on Ganoids thus far enumerated have been made upon Lepidosteus. In Acipenser, Salensky ('78, '80) maintains, in opposition to Kowalewsky, Owsjannikoff and Wagner ('70), that the excretory organs first appear as a differentiation in the form of a solid cord of cells. There is at that stage no trace of the cœlom, nor of a division into protovertebral and lateral plate. Indeed, this cord of cells first marks the region where the latter separation will later occur. In its further development the cord of cells acquires a lumen, either by a rearrangement of the cells, or by destruction of the axial ones. Anteriorly the structure now opens into the body cavity. The anterior portion elongates and becomes more and more convoluted up to the time of "post-embryonic" development. Opposite each of the peritoneal funnels are formed glomeruli [glomi] as processes from the radix mesenterii. They are covered by a pigmented layer of peritoneum. Salensky does not seem to me to have been very clear upon the earliest development, which was studied mainly by surface views, and I am of opinion that these stages would show very different conditions if more recent technical methods were employed. The most interesting feature of the development, as described by Salensky, is the occurrence of a glomus in the position which is typical for Amphibia and Petromyzon.

The excretory system has probably been studied more carefully in Selachii than in any other group. The independent researches of Balfour ('75 and '78) and Semper ('74 and '75) are in substantial accord, and have formed the basis for all subsequent investigations. For our purpose, the most prominent feature of the development as described by these authors is the absence of any structure which demonstrably represents the pronephros. According to Balfour, the first trace of the excretory system appears as a solid knob springing from the "intermediate cell mass" near the level of the hind end of the heart. From this anterior proliferation a solid cord of cells grows backward between ectoderm and mesoderm. The posterior portion is the fundament of the segmental duct; the anterior knob persists in adult females as the ostium abdominale of the oviduct. According to Balfour, this solid knob represents a rudimentary pronephros.

Very recently the early development of the excretory organs has been placed in a new light by the researches of Rückert ('88) and van Wijhe ('89). According to Rückert, the development begins with the formation of a pronephros as an outgrowth towards the ectoderm from the ventral portions of several *protovertebræ*, extending from the third or fourth trunk somite backwards for a distance of four to six somites. The thickening extends ventrally in each somite to the region where the segmented mesoderm passes into the unsegmented lateral plates. The proliferation, in the formation of which the somatic layer is alone concerned, shows on careful study a metameric character. From the posterior end of each protovertebra a narrow canal can be traced outwards and backwards, where it unites with a similar canal emerging from the next following somite. The pronephric mass fuses for a time with the ectoderm and probably receives a contribution of cells from that layer. The duct grows backwards as far as the cloaca at the expense of the ectoderm. Having reached this stage of development, the pronephros rapidly degenerates. This process takes place in a slightly different way in the anterior and posterior regions. A variable number of the most anterior evaginations flatten out into a simple longitudinal groove of peritoneum, the ostium abdominale; the remaining ones become closed and detached from the peritoneum; thus there remains a longitudinal canal communicating with the body cavity by the slit-like ostium. In interpreting the structure as a rudimentary pronephros, it is important to note the discovery by Rückert (pp. 239–242) of a structure which he regards as a pronephric glomerulus, or glomus. This structure is developed in connection with segmental blood-vessels which pass from the aorta to the right subintestinal vein, and which have been described by Paul Mayer ('87, p. 343). In Torpedo the vessels are present on the right side in the same number as the segments of the pronephros, and as they pass ventrally between the entoderm and the splanchnopleure it is to be noticed, in regard to the middle vessels at least, that they send out buds, which form projections from the median peritoneal wall opposite the pronephric tubules.

It will be at once seen that the development of the pronephros as described by Rückert is in striking agreement with the account I have given of the early stages in the development of the Amphibian pronephros, and I have no hesitation in homologizing the two organs. The earliest stage which has been observed in both groups is that which I have termed the pronephric thickening. This is followed in both by the stage of canalization; but the Selachian pronephros never goes beyond an early condition of the pronephric pouch, in which, however, the homologues of the nephrostomal tubules and the collecting trunk appear. The points of difference between the account I have given and that given by Rückert for corresponding stages of the Selachian pronephros seem to me, with a single exception, to be either unreal or insignificant. The exception to which I refer pertains to the participation of the ectoderm in the formation of the pronephric thickening. This condition I am confident does not occur in Amphibia. Moreover, the evidence upon which Rückert bases his statement seems to me far from conclusive, nor has his observation been confirmed by any subsequent investigator. Rückert described the pronephric thickening as a product of the protovertebræ. I cannot admit that this is true for Amphibia; but I believe that our differences of opinion are really due to the fact that we use different criteria for determining the boundaries of the protovertebræ. There can be no doubt that the earlier pronephric thickening is made up of metameric constituents; but I should be unwilling to regard all segmented mesoderm as belonging to the protovertebræ. On the contrary, I am of opinion that the ventral extent of the protovertebræ is for the first time defined when the longitudinal constriction appears which divides the primitive cœlom into protovertebral cavity and pleuroperitoneal or (secondary) body cavity. When such a definite line of demarcation has been established, the remnant of the pronephros in Selachii, as well as the functional pronephros in Amphibia, remains connected with the latter space. The remaining points of difference relate to the number of tubules involved, — which, as we have seen, varies even within the class of Amphibia, — and to their position with reference to the somites. The latter feature seems to me to be at once difficult to determine and of minor importance.

Before the conclusion of this paper I shall endeavor to indicate how the glomus of Amphibia may possibly have been derived from the type of structure which is described by Rückert for Selachians and by Boveri ('90) for Amphioxus.

The results gained by van Wijhe ('89) do not seem to me to differ from those of Rückert in many respects which are of importance for a comparative study. The great divergence of their descriptions in the case of many details seems to me to be occasioned mainly by the peculiar conception which Rückert holds of the relations between the protovertebral and the lateral mesoderm. For these details and for the hotly contested questions of priority, I must refer to the original papers (van Wijhe, '86, '87, '88^a, '88^b, '89, Rückert, '88, '89), and consider here those features only which merit special attention because of their bearing on the general questions of homology. Van Wijhe denies positively the participation of the ectoderm in the formation of the pronephric thickening; and he claims that the ostium abdominale is formed from the pronephros by the fusion of the nephrostomes. Finally, structures which are supposed by him (pp. 480–482) to represent the pronephric glomeruli of Rückert are described as occurring on both sides of the body, not, as affirmed by Rückert, on the right side alone, and van Wijhe inclines to the view that they are actually equivalent to the glomi of Amphibia. The body described by van Wijhe consists of a vascular rod, which passes obliquely from the dorsal to the ventral lip of the pronephric pouch, and represents the last trace of the partition between two peritoneal openings, which have not yet fused. Rückert's description is not entirely clear, and also suffers from misleading typographical and grammatical errors; but it is certain that the structure he describes lies within the splanchnic peritoneum, and is not to be confounded, as was done by van Wijhe, with the partition between two pronephric tubes. Rückert says ('88, p. 239), "Es [ein Paul Mayer'sches Quergefäss] zieht dicht an der medialen Grenze der Vornierenanlage vorbei und gelangt, indem es die Leibeshöhle durchbricht, d. h. ihre Wandung vor sich herstülpt, an die Aussenfläche des Darmes, wo es zwischen Ectoderm [soll wohl Entoderm heissen] und Splanchnopleura gelegen, mit der rechten Subintestinalvene confluirt." I cannot admit that the structure described by van Wijhe is the homologue of the Amphibian glomus, nor do I believe that it corresponds to the structure observed by Rückert.

The mode of development of the excretory system is much alike in the three groups of Amniotes. It seems, however, best in the present instance to deal with the Reptiles separately from Birds and Mammals. The most important of the works on the Reptilian excretory system is perhaps the monograph of Braun ('77), which, however, is of little service in elucidating the earliest stages. Weldon ('83) first gave a satisfactory account of the early development. According to this author, the first trace of the excretory system in Lacerta is found in the region of the intermediate cell mass, and consists of a series of vesicles (Segmentalbläschen of Braun), which have a strictly metameric arrangement. Throughout a region of five protovertebræ (from the 8th to the 12th), there appears on the external wall of these segmental vesicles a rod of cells at first composed of discontinuous parts. This rod is the fundament of the segmental duct; in the region between two successive protovertebræ, it is budded off from the unmodified "middle plate" (Waldeyer), or intermediate cell mass. Behind the twelfth protovertebra, the duct grows backward, free from adjacent tissue. The rod of cells soon acquires a lumen, continuous anteriorly with the cavities of the segmental vesicles.

The observations of Mihalkovics ('85) upon Lacerta agilis differ from those of Weldon mainly in two particulars. In the first place, according to Mihalkovics (pp. 42, 43), the most anterior three or four pairs of segmental vesicles at the time of their origin communicate both with the body cavity and with the protovertebral cavity. In other words, they are formed as expansions of what I have termed the communicating canal, or Mittelplattenspalten of the German authors. Some somites in the series, however, may be without vesicles. Secondly, Mihalkovics (p. 48) maintains that the segmental duct buds off from the middle plate as a *continuous* cord of cells at a time when only the first trace of the segmental vesicles has appeared. Before the (3 or 4) anterior segmental vesicles have entirely lost their connection with the body cavity, they communicate distally with the lumen of the segmental duct, and may therefore be regarded as typical nephrostomal canals. This condition is never encountered in the posterior vesicles, which develop independently of the cœlom in the solid Wolffian blastema, or middle plate. In consequence of this difference in the mode of development of the anterior and posterior portions, Mihalkovics is of opinion that the first three or four segmental vesicles represent a rudimentary pronephros.

According to Strahl ('86), the segmental vesicles are budded off from the ventral portions of the protovertebræ, and gain secondarily a connection with the body cavity; the duct does not appear until the vesicles are evident.

Ostroumoff ('88^b, p. 81) confirms for Phrynocephalus the observations of Mihalkovics regarding the anterior segmental vesicles, although he is unable to ascertain the precise number that communicate with the body cavity. He also interprets these anterior vesicles as a pronephros. The duct, however, first appears in disjointed fragments lying between successive vesicles.

According to Hoffmann ('89), there develops in Reptiles a pronephros similar to that described by Rückert ('88) for Selachii. It appears as a series of evaginations of the somatopleure. These are formed in the region where the protovertebræ pass over into the lateral plates. The organ extends over a variable number of somites (6–7 in Lacerta and 5–6 in Tropidonotus). As protovertebræ separate from the lateral plate, the pronephric evaginations remain in connection with the former, except in the case of the first outgrowth (L. agilis, in L. muralis the first two), which forms for a time a single pronephric ostium. The most posterior outgrowth extends backwards, and forms the fundament of the segmental duct. The fate of the several evaginations is different. The most anterior and possibly the next following outgrowth abort at an early stage; the remaining evaginations become detached from the protovertebræ and fuse with one another, thus forming a tube closed in front, but continuous posteriorly with the segmental duct. Hoffmann identifies these evaginations with the segmental vesicles of Mihalkovics and Weldon, but asserts that these authors mistook for a separate fundament of the segmental duct a blind backward prolongation of the evagination belonging to the immediately preceding somite. These backward processes are described by Rückert for Selachii. Ostroumoff's ('88^b, pp. 78, 79) statement, apparently unknown to Hoffmann, that the duct first appears in short fragments, each of which lies posterior to a segmental vesicle, could be readily brought into accord with these observations.

In regard to the correctness of Hoffmann's conclusions that these evaginations represent a pronephros, I am of opinion that there is considerable room for doubt. The organ described by Hoffmann differs in two important respects from that of Selachii, and from the young stages of the Amphibian pronephros as presented in the first part of this paper. In the latter groups, while the metameric evaginations are yet continuous with the cœlom, they have also fused distally to form a longitudinal canal (collecting trunk); this condition I wholly miss in Hoffmann's account, according to which all the evaginations remain distinct from each other till they have entirely separated from the cœlom, and only the more posterior outgrowths ever fuse together. Secondly, no structure comparable to the Amphibian glomus is described. The latter objection would apply equally to the account given by Mihalkovics.[1] None of the previous investigators were more successful in finding glomeruli of the pronephric type.

In regard to the former feature, however, the account of Mihalkovics is more satisfactory, since the most anterior three pairs of vesicles stand in precisely this relation to the body cavity and to the collecting trunk (segmental duct). In reviewing Mihalkovics's interpretation, Hoffmann says ('89, p. 272), since "die Vorniere als eine Ausstülpung, die Urniere nicht als solche entsteht, kommt es mir höchst wahrscheinlich vor, dass die Vermuthung von Mihalkovics, nach welcher die proximalen Urnierenkanälchen der Eidechsen der Vorniere der Amphibien entsprechen, eine andere Deutung zulasse." I judge from this passage that Hoffmann is inclined to regard as mesonephric tubules the anterior three or four segmental vesicles described by Mihalkovics. I am quite unable to harmonize this view with Hoffmann's prior identification ('89, pp. 267, 268) of the pronephric evaginations described by him with the segmental vesicles of Mihalkovics and Weldon. The mode in which the mesonephric tubules develop in Lacerta is asserted to be very similar to that described by Rückert and van Wijhe for Selachii. If I properly understand Hoffmann's description, the space lettered *c.* in Tafel XVII. Figs. 3 and 4, is the lumen of a mesonephric tubule. From these figures it is evident that the mesonephric tubule develops from a portion of mesoderm ventral to the pronephros; but according to both Rückert and van

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[1] Figures 18 and 19, referred to by Wiedersheim ('90^b, p. 413) in this connection, do not relate to Reptiles at all. They represent sections of Duck embryos.

Wijhe, the mesoderm which produces the mesonephric tubules in Selachii belongs to a region dorsal to that which gave rise to the pronephros (see the diagrams appended to van Wijhe, '89, Taf. XXXII.).

In view of the difficulties to which I have alluded, it seems to me that Hoffmann's position cannot be regarded as satisfactory. Furthermore, if Hoffmann's observations[1] on the origin of the posterior mesonephric tubules be accurate, the contrast which Mihalkovics endeavored to establish between the anterior and posterior tubules does not exist. If, finally, these anterior three or four pairs of tubules develop in their course typical Malpighian capsules remote from the peritoneum, — Mihalkovics is not clear on this point, — I can see no reason for regarding them as pronephric. I am therefore of opinion that there is at present no evidence which *proves* a pronephros to exist either in Lacertilia or in Ophidia.

It remains for me to consider two recent papers by Wiedersheim ('90^a, '90^b), which describe a very interesting condition of the excretory system in Crocodilia and Chelonia. The anterior portion of the embryonic excretory organs in these groups consists of a number of tubules which take their origin in ciliated nephrostomes, and, after undergoing contortion, join a longitudinal canal continuous with the segmental duct. From the root of the mesentery a large glomus protrudes into the body cavity. It lies in a distinct fold of the peritoneum, and consists of a mass of highly vascular tissue receiving distinct vessels from the aorta. It extends continuously opposite a number of nephrostomes, and is evidently equivalent to the Amphibian glomus. In somewhat more posterior regions the conditions are essentially the same; but the nephrostomes and the glomus having approached each other, they are cut off from the main portion of the body cavity by a longitudinal fold of peritoneum. In this manner, there is formed a pronephric chamber comparable to that of Amphibia. In yet more posterior regions, the pronephric chamber with its contained glomus breaks up into a series of capsules containing glomeruli, each of which then appears to form the blind termination of a tubule. This is the region of the mesonephros with typical Malpighian capsules. In the subsequent development of the embryo, the anterior portion of this excretory system early atrophies, and the hinder part alone constitutes the well known Wolffian body, or mesonephros. In my opinion, the account given by Wiedersheim affords a satisfactory basis for the view that the most anterior portion of this excretory system is truly pronephric. It seems, however, quite impossible to draw a rigid line between pronephros and mesonephros. Indeed, such is a part of the conclusion which I think we shall finally be able to draw from the entire review.

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[1] Similar observations are recorded by Orr ('87, pp. 325–327).

The numerous accounts which have been recently given of the pronephros in the higher Amniota may be conveniently treated under three heads: —

(1.) According to Balfour and Sedgwick ('78, '79), the Müllerian duct in the Chick first appears in a region somewhat behind the front end of the Wolffian duct as three slender invaginations of the peritoneum which covers the Wolffian body. These invaginations later fuse at their distal extremities, and the most posterior involution grows backwards in connection with the Müllerian duct. There is thus formed a longitudinal canal with three peritoneal funnels, the whole structure being comparable to the pronephros of Amphibia. Slightly in front of the nephrostomes there is attached to the radix mesenterii a vascular body which resembles the Amphibian glomus. It receives blood-vessels from the aorta, and projects into the body cavity enclosed in a distinct sac of peritoneum. Gasser ('74, pp. 58, 59) had previously observed somewhat similar conditions in the anterior end of the Müllerian duct; and, by renewed investigation, Gasser and Siemerling were able to confirm the occasional occurrence of the phenomenon, though a single invagination appeared to be the rule. Multiple invaginations have also been mentioned by Kollmann ('82^b, p. 20), Siemerling ('82, p. 29), Janošik ('85, p. 43), and Mihalkovics ('85, p. 295); but Braun ('79) and Renson ('83, p. 37) were unable to find any evidence of such a condition. Braun also opposed Balfour and Sedgwick in their view respecting the nature of the vascular body, and Sedgwick ('80^b) later came to the conclusion that this structure was really a series of greatly modified mesonephric glomeruli. This interpretation was adopted by Balfour ('81^a, p. 590).

(2.) The second view is set forth in the recent account of Felix ('90), who describes in a chick embryo with eight protovertebræ a series of outgrowths, which, emerging from the lower hinder portions of protovertebræ IV.–VIII., extend backward and outward toward the ectoderm. The latter layer occasionally presents local thickenings in this region, and in some cases a connection between the mesodermal outgrowths and the ectodermal thickenings can be observed. In older embryos no trace of the structures can be found. As was the case with the evaginations found by Hoffmann ('89) in Reptiles, no fusion of their distal extremities is recorded. This condition makes them at once unlike the Selachian pronephros described by Rückert, and the early stages of the Amphibian pronephros as detailed in the preceding pages. Moreover, Felix produces no evidence to show that they stand in any genetic relation whatever to the Wolffian duct, or to the pronephric structures described by other authors. In the present state of knowledge his interpretation seems to me untenable.

(3.) The remaining views all have the common feature that they regard certain rudimentary canals in connection with the anterior end of the Wolffian duct as pronephric. The views are somewhat divergent, but I have been able to compile from them a general statement which will in a measure explain their conflicts. In bringing the observations of each author under this general scheme, I shall frequently be driven to regard his results as incomplete, but I shall as far as possible avoid questioning his statements from an *a priori* standpoint.

In general three regions of the embryonic excretory organ may be distinguished: the pronephros, an intermediate region, and the mesonephros. For criteria of these regions, I shall use in the main glomerular structures: those of the pronephros are glomi wholly external to the tubules; those of the intermediate region are transitional glomeruli, which develop in peritoneal canals, but project through the nephrostomes into the body cavity; those of the mesonephros are typical glomeruli, which have only a mediate connection with the body cavity through the tubule.

It now remains to consider the results of the observers whom I have placed in my third group. The work of Gasser and Siemerling ('78, '79), subsequently carried on by Siemerling ('82), relates to Birds alone. These authors recognize two distinct portions of the Wolffian duct: a portion lying in front of the fifth somite, and a posterior portion. The former shows many irregularities, is broken up into discontinuous fragments, and early atrophies; the latter develops more slowly, but more regularly, and persists as the duct of the Wolffian body. The first indications of tubules consist of the so-called primary cords, which are continuous with the cœlomic epithelium by means of funnel-shaped ostia, while they are distally in contact with the duct. Gasser and Siemerling maintain that they belong to the most anterior part of the mesonephros, a portion which early atrophies. They are quite similar to the S-shaped canals of Kölliker ('79). In front of the region of the "primary cords" similar evaginations occur, but these never reach the duct. A typical glomus, which may be single or may be divided into parts, projects from the radix mesenterii opposite the openings of these evaginations. In embryos of this stage the space between the most anterior Wolffian tubule and the pronephric structures is traversed by a series of glomeruli which resemble most closely those of the mesonephros. Siemerling calls them transitional glomeruli. The pronephros of our scheme would be represented in this account by the region in front of the fifth protovertebra; the intermediate region would correspond to the space occupied by the transitional glomeruli, and also, as I believe, to that previously occupied by the primary cords; the mesonephros would form the rest of the organ.

According to Sedgwick's ('81) account of the development in the chick, the Wolffian duct, in separating from the proliferation in which it arises (region between the 7th and 11th protovertebræ), remains connected with the peritoneal epithelium by short cords of cells. Between the 8th and 15th protovertebræ, the duct, as it grows freely backwards, comes secondarily into contact with such a cord of cells in each somite. Behind the 15th somite, the fundaments of the tubules (intermediate cell mass) do not join the duct until their differentiation is somewhat advanced. The cords of cells in the region between the 7th and 11th protovertebræ acquire lumens which may be continued even into the duct; but both cords and duct soon entirely disappear. Although no glomus is described, this region probably represents the pronephros. Between the 12th and 15th protovertebræ typical nephrostomal funnels are formed, in which transitional glomeruli develop. This portion of the organ would then correspond to the intermediate region of the general scheme; behind this region comes the typical mesonephros. Sedgwick regarded the first mentioned region as pronephric; but he hoped to be able to harmonize such a view with the position (*cf.* page 276) formerly taken by himself and Balfour (Balfour and Sedgwick, '79).[1]

In the foregoing description I have assumed that the most anterior portion of the Wolffian duct and the accompanying transverse canals observed by Sedgwick corresponded to the pronephric region as described by Siemerling. This interpretation seems to me in all probability correct; yet it should be recalled that the pronephros described by Siemerling lies in front of the 5th somite, and is anterior to the region in which the early proliferation to form the duct took place; whereas, the pronephros, according to Sedgwick, lies between the 7th and 11th protovertebræ and arises in the same region in which the duct first appears.

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[1] Mihalkovics's statement, that Sedgwick abandoned his former view, is incorrect, as will be seen by referring to the closing paragraph of his article (Sedgwick, '81, p. 468).

In the second edition of Foster and Balfour's ('83, p. 218) Elements of Embryology, revised by Sedgwick and Heape, the anterior end of the Müllerian duct is the only homologue of the Amphibian pronephros suggested.

Lockwood ('87, pp. 657–663) describes three regions in the embryonic excretory organ of the Rabbit. In the most anterior region (pronephros), the duct consists of isolated fragments, which are connected with the body cavity by 2–3 nephrostomes. Then follows a region of typical nephrostomal canals with glomeruli, and finally typical blind mesonephric tubules. Possibly the last two regions belong to the mesonephros; but in none of the accounts of Mammalian development have I been able to recognize with certainty the intermediate region.

According to Renson ('83, p. 29), glomeruli develop in the Chick in the region of the pronephros, which is otherwise described in agreement with Sedgwick's account. The pronephric tubules atrophy with the exception of their nephrostomes, and in the hollow of each funnel there appears a glomerulus which soon comes to project freely into the body cavity. In a region directly posterior to that in which the free glomeruli occur, there are found the so-called mixed glomeruli, which are situated in the base of an infundibular depression, and are partially covered by a fold of peritoneum. This, as well as the more anterior portion of the system, Renson regards as belonging to the pronephros. He also describes in the Rabbit a series of peritoneal involutions in connection with a discontinuous duct. In this region he likewise observed a vascular structure, which he regarded as a very rudimentary external glomerulus. A similar observation has been recorded for human embryos by Lockwood ('87, pp. 662, 663), and for Arvicola by Spoof ('83, p. 86, footnote). It is difficult to arrive at a satisfactory estimate of Renson's position. There would be no difficulty in classing him with Sedgwick, were it not for the circumstance that he describes for the pronephric region (6 or 7th to 11 or 12th somites) glomerular structures which, according to his own comparison, develop in the same way as the transitional glomeruli observed by Sedgwick in the "intermediate" region only (11th to 14th somite). If, however, it should prove to be true that only the "mixed" glomeruli develop in this way, the conflict would at once be removed, and Renson's account would show the three primary regions in their typical condition.

According to Mihalkovics the most anterior two or three tubules (4–7 somites) in the Chick and Duck are derivatives of the communicating canals, and gain a connection with the duct while yet opening into the body cavity by a distinct ostium. The posterior canals, on the contrary, are all differentiated from the solid "Wolffian blastema," and never have any connection with the body cavity. Posterior to the last pronephric canal, 5–6 free glomeruli are to be found. The anterior canals form much earlier than the posterior, indeed they wholly abort before the mesonephros attains its final development; and they together with the free glomeruli are, in his opinion, to be regarded as equivalent to the pronephros and glomus of Amphibia. Mihalkovics also mentions the occurrence of transitional glomeruli; these are typical glomeruli which lie near the peritoneal covering of the Wolffian body. It seems to me probable that these glomeruli really belong to the mesonephros, and that at least a portion of the "external glomeruli" belong in reality to the class which I have designated transitional glomeruli. This interpretation would not merely be in agreement with the described position of the glomeruli with reference to the somites, but it would also accord well with the figures Mihalkovics gives of the two sets of glomeruli. Thus, in his representation of a transitional glomerulus (Taf. I. Fig. 17, *g. m.*), there is little reason to regard the structure as in any way different from a mesonephric Malpighian body. I may here further remark, that nearly all other modern investigators agree in deriving a part, if not all, of the mesonephros from a layer of cells which primitively bounded the cœlom, rather than from a strictly indifferent blastema. In this light, the validity of the principal contrast Mihalkovics sought to establish between the pronephros and mesonephros becomes at least very uncertain.

The account of Janošik ('85) affords the best basis for the general scheme I have proposed. The most anterior region, or pronephros, develops somewhat *later* [!] than the first tubules of the mesonephros (primary cords?). The duct in the region of the pronephros is broken up into fragments, which receive rudimentary peritoneal canals. Three typical glomi are developed on the radix mesenterii. In the next following region (intermediate), from two to five peritoneal canals communicate with the Wolffian duct. Near the nephrostomal ends of these canals transitional glomeruli develop. Both the pronephros and the intermediate region rapidly atrophy. The remaining portion of the embryonic excretory organ is the true mesonephros. The mesonephric tubules are either developed as separate buds from the peritoneum, or are differentiated from a blastema which is directly derived from the peritoneum. Janošik was able to confirm Renson's discovery of rudimentary pronephric tubules in the Rabbit, but was unable to find in this form any trace of external glomeruli. Later, however, he ('87, p. 582) described in a young human embryo, 3 mm. in length, a peculiar projection into the body cavity. The structure resembled the external glomerulus of Birds, and he was inclined to interpret it as such in this case.

In the preceding pages I have endeavored to present a comprehensive résumé of the development of the pronephros as described in groups of Vertebrates other than Amphibia. In this review it has been shown that an equivalent of the Amphibian pronephros has been claimed to exist in all Craniota; and that a mode of development similar to that described in the early part of the present paper has been found in Selachii by Rückert ('88) and van Wijhe ('89), in Petromyzon by Kupffer ('88), and in Lepidosteus by Beard ('89). The Reptilian pronephros as described by Hoffmann ('89), and that of the Chick according to the account of Felix ('90), do not seem to me to be in perfect accord with this mode of development.

It now remains for me to compare the results of my studies, as detailed in the descriptive part of the present paper, with those which have been recorded by other writers on the development of the Amphibian pronephros. According to the account which at present receives most general acceptance, the pronephros first appears as an outfolding of the somatopleure in the form of a longitudinal groove. The anterior end of this groove is destined to become the pronephros; the remaining portion is constricted off to form the segmental duct. Since the process of constriction advances from before backwards, stages may be found in which a completed tube is continuous posteriorly with a mere groove of the somatopleure. In the anterior region, the groove remains in communication with the body cavity, and grows down towards the ventral surface of the embryo in the form of a broad pocket. The slit-like peritoneal opening of this pouch closes throughout the greater part of its length, leaving, however, two or three regions of incomplete closure, the fundaments of the nephrostomes. The nephrostomal tubules are formed by the fusion of the walls of the pouch between two nephrostomes. The regions of fusion extend in vertical lines from the nephrostomal margin of the pouch nearly to its ventral border, where there is left an unfused and therefore continuous longitudinal tract constituting the canal which I have called the collecting trunk. This view of the development of the pronephros, although suggested by Wilh. Müller ('75), was first described in detail by Goette ('75) for Bombinator, and was later extended to other Amphibia by the researches of Fürbringer ('77). It has been entirely confirmed by Wichmann ('84), by Hoffmann ('86), and still more recently by Marshall and Bles ('90^a).

In opposition to this view, I would maintain: (1) that the first trace of the excretory system consists of a solid proliferation of somatopleure, the pronephric thickening; (2) that the lumen of the system arises secondarily; and (3) that the pronephric tubules do not appear in consequence of the local fusion of the walls of a widely open pouch, but that they are differentiated at an early stage from the hitherto indifferent pronephric thickening.[1]

The development of the pronephros and duct from a solid mass of mesoderm was a common feature in the accounts of those who wrote prior to Wilh. Müller and Goette, but since then this mode of origin, though repeatedly maintained by single observers, has failed to gain general acceptance. Clarke ('81) described a solid pronephric thickening, and asserted that the lumen arose secondarily in this mass; the details of the process are, however, not accurately given. Duval ('82) also described the pronephros as first appearing in the form of a solid thickening. He however states that it later acquires a slit-like opening into the body cavity, and that by the imperfect closure of this opening the successive nephrostomes are formed, as described by Goette and Fürbringer. This latter statement I am unable to confirm. Gasser's ('82, pp. 89–97) short note gives, on the other hand, an account of the early development in Alytes, which is in substantial agreement with my own observations. His account of the first differentiation of the nephrostomal canals is not very full, but it is not improbable that he conceived it to take place in a manner altogether similar to that which I have described. His statements seem to me in general correct,[2] but incomplete.

Janošik ('85, p. 19) states, on the basis of personal observations, that the first trace of the segmental duct in Bufo and Triton is a solid mass of cells, which he is, however, inclined to regard as a disguised fold of somatopleure.

According to a recent account by Kellogg ('90), a lumen does not appear anywhere in the organ (except in the region of the nephrostomes) until it has been separated from the peritoneum. Finally, Mollier ('90, Rückert and Mollier, '89) has published an account of the early development, which is for the most part in close accord with the results of my own studies. Since these results were gained entirely independently of

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[1] The large cavity which the pronephric pouch presents in Stage IV. of Rana and Bufo is a secondary condition produced by the expansion of the lumens of the several diverticula.

[2] I must here except his statement that the second tubule is differentiated before the rest; this I believe to be an error.

Mollier's researches and were written out before his paper came into my hands, it seems to me that my confirmation of his position affords excellent evidence of the correctness of the view advocated. In one feature alone our accounts of the earliest condition of the pronephros would seem to differ widely, but I am confident that the difference is apparent rather than real. Mollier states that each of the diverticula which form the first indications of the nephrostomal canals emerges from a protovertebral cavity. This statement, as I have already shown, does not in my opinion accurately represent the actual conditions. In the stage under consideration, the dorsal portion of the mesoderm is in the anterior region divided by transverse planes into a series of metameric blocks; the pronephric thickening also is made up of metameric constituents, and is continuous dorsally in Amblystoma with two, in Rana and Bufo with three, of the blocks of mesoderm. As yet no definite line can be drawn between the protovertebræ and the lateral plates; in a slightly older embryo, however, the protovertebræ begin to be constricted off from the lateral plates, and it is at once evident that the pronephric tubules have to do with the ventral segment of the mesoderm. This difference in our accounts seems to me then very trivial, and my only excuse for dwelling upon it is the circumstance that Rückert and Mollier seem to attach great morphological significance to this feature of their account. This relation to the protovertebræ seems to me quite untenable.

Previous authors have been singularly reticent respecting the exact position of the pronephros with reference to the body somites. Fürbringer ('78ᵃ, p. 5) states that the pronephros of Anura extends over three, that of Urodela over two somites; but I have looked in vain for a statement which should show whether the nephrostomes are segmental or intersegmental in position. Kellogg states that each nephrostome occurs opposite the middle of a protovertebræ. Marshall and Bles confirm this statement, and contend that, in the case of Rana, the nephrostomes lie in the 2d, 3d, and 4th somites behind the auditory vesicle. According to Mollier ('90, p. 213) the pronephros appears in Triton in the region of the 1st and 2d trunk protovertebræ; but since the most anterior two protovertebræ are reckoned to the posterior region of the head, these represent the 3d and 4th protovertebræ of the series. The enumeration which I have given for Rana and Bufo is in precise agreement with that of Marshall and Bles. For Amblystoma my account is in agreement with that of Mollier for Triton.

I am not aware that any definite attempt has thus far been made to ascertain which of the three nephrostomes of Anura is unrepresented in

Urodela. At first sight it would seem probable, — and by implication I accredit this opinion to Mollier, — that the rudimentary third tubule occasionally present in Urodeles corresponds to the normal third tubule of Anura. This view, however, is not in precise harmony with the relations of the nephrostomes to the myotomes. As I have already shown, the first nephrostome in Amblystoma is situated beneath myotome III., whereas in Rana and Bufo it occurs under myotome II. If now the enumeration of the somites in the two cases correspond, it follows that the first and second nephrostomal tubules of Amblystoma are equivalent to the second and third tubules respectively of Rana and Bufo, not to their first and second tubules, and that the occasional rudimentary third tubule of Urodeles belongs to a more posterior somite, and is unrepresented in Anura. In Amblystoma the root of the vagus nerve arises immediately in front of the somite which I have denominated I.;[1] the same is true in the case of Rana and Bufo, and I am inclined to regard these as equivalent somites. It is possible that somite II. of Amblystoma is not represented in Rana and Bufo; but this is hardly probable, since it belongs to the head region, which is hardly likely to vary in such closely related groups, and since it is evident that the greater number of protovertebræ present in Urodeles as compared with Anura is largely accounted for by additional protovertebræ in posterior regions, particularly in the region of the mesonephros, as I believe. In general, it seems to me that we should be more ready to admit the abortion of the most anterior tubule in Urodela than to assert the existence of an additional protovertebra in Anura.

All the more recent writers are agreed that in Anura three pairs of pronephric nephrostomes occur, Giles ('88, p. 135) alone claiming that a degenerating pronephros may have four. In Urodela the typical number is two; but Mollier ('90, p. 224) has recorded the occasional occurrence of three pairs in Triton, and I have made similar observations in Amblystoma. Spengel ('76, p. 19, Taf. II. Fig. 21) maintained, on the evidence of a specimen in which the pronephros was largely degenerated, that four pairs occur in Cœcilia; the recent observations of Semon ('90, p. 462), on the other hand, have shown that there exist in Ichthyophis on *each* side of the body ten *pairs* of nephrostomes, therefore forty in all.

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[1] Somite I. of this enumeration probably corresponds to the one which has been called somite XI by Houssay ('91). Houssay believes that he can identify in Amphibia the somites which have been observed in the head region of Selachii. If his conclusions are accurate, they are evidence in favor of the view that this region of the body is very permanent.

Of the two nephrostomes belonging to any pair, one opens freely into the body cavity, the other communicates with a pronephric chamber, which contains the glomus and is completely shut off from the body cavity. The meaning of this condition I shall consider in the subsequent discussion. The pairs of nephrostomes on each side are slightly more numerous than the overlying protovertebræ.

The origin of the so-called ventral part (common trunk) of the pronephros has recently become the subject of controversy. According to Goette the duct at first communicates with the posterior end of the widely open pronephric pouch. At the same time that the nephrostomal canals are formed by local fusions of the walls of the pouch, a similar process constricts off the posterior ventral portion of the pouch; this has the effect of lengthening the duct, so that the point of its attachment is carried forward to the place where the converging nephrostomal tubes unite. The portion of the longitudinal canal in front of the most posterior nephrostome represents the "ventral part" of the pronephros.

According to Fürbringer, the longitudinal groove which forms the earliest fundament of the pronephros and duct becomes entirely constricted off from the somatopleure as far forward as the opening which leads into the pronephric pouch; this slit-like opening then elongates posteriorly, so as to extend into the region formerly occupied by the longitudinal canal alone; the latter thus comes to lie ventral to the last nephrostomal canal, and forms the ventral part of the pronephros.

Kellogg ('90) opposes the accounts of previous observers, and claims that the ventral part "is formed from the ventral side of the dorsal part of the pronephros, and *anterior to the last nephrostome*." Marshall and Bles, alluding to Kellogg's description, declare that it is in exact accordance with the accounts of Goette and Fürbringer. I have not been able to satisfy myself as to the precise manner by which Kellogg conceives the formation of the ventral part to have taken place; but I think he has said enough to contrast his position strongly with that of Fürbringer, according to whom the ventral part of the pronephros first appears as a portion of the somatopleural fold immediately *posterior* to the part which gives rise to the nephrostomal canals. Kellogg argues, however, that, were the views of previous authors correct, some portion of the pronephros would appear behind the last nephrostome; but this is actually never the case. The force of this argument I am wholly unable to appreciate, and I must in consequence feel some doubt as to whether I have properly interpreted Kellogg's previous statements.

According to Mollier, the "ventral part" is differentiated in the ventral portion of the broad pronephric thickening. Mollier's description is substantially in accord with my own observations, and it seems to me probable that Kellogg's statements are to be understood in the same way.

The structure of the functional pronephros was early the occasion of much controversy. The discoverer of the organ, Joh. Müller ('29 and '30), describes and figures it as a cluster of blind tubules, which radiate in the form of a rosette from the anterior tip of the segmental duct. This view was shared by the larger number of the early investigators. According to von Wittich ('52), the gland is typically formed by the convolutions of a single tube; in the more complicated pronephridia, however, this canal may give off branches. It is to Goette and Fürbringer that we owe the first accurate account of the process of convolution.

According to these authors, the gland is composed of two portions: a "dorsal part" (collecting trunk and nephrostomal canals), which alone receives the nephrostomes,[1] and a "ventral part" (common trunk), which serves as the efferent canal, and is in communication with the anterior end of the segmental duct. Both ventral and dorsal parts undergo extensive convolutions, and give rise to blind diverticula. Subsequent authors have in general confirmed Fürbringer's account, but have added no new matter to the description. Selenka ('82) describes and figures an interesting condition of the pronephros in Hylodes. The glands of the two sides are unsymmetrical, and depart widely from the typical structure known in Amphibia. Following the nomenclature which I have proposed in the descriptive part of this paper, it is evident that the nephrostomal canals and the collecting trunk are present, but do not show the convolutions customary in these parts. The "ventral part" of the gland, however, is not formed by the windings of the common trunk, but is composed of great irregular blind pouches which communicate with the collecting trunk, while the latter opens *directly* into the anterior end of the segmental duct. This condition of the pronephros evidently represents the degeneration of the gland, and Selenka is inclined to correlate the premature appearance of this complication in Hylodes with the absence of gills in the larvæ of this form.

Kellogg has studied the structure of the pronephros in Amblystoma and Rana by means of reconstruction from cross sections. His preliminary notice, however, does not describe the process of convolution in detail. An interesting feature is the statement that blind diverticula do not appear until the tubes of the gland have become very much convoluted. In the pronephridia which I have studied, I have never seen a blind diverticulum. My observations do not extend to sufficiently old stages to allow me to deny that such diverticula appear anywhere in the developmental history of the gland, but the organ can reach at least the high degree of complexity shown in Figures 41 and 65, and yet be composed of the windings of the nephrostomal canals, the collecting trunk, and the common trunk without possessing any blind diverticula.

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[1] Duval ('82, Fig. 7), figures the second pronephric nephrostome in Rana as opening directly into the ventral part of the gland. I have never seen such a condition in my preparations, nor do I know of similar observations being elsewhere recorded. It seems likely that Duval has here fallen into error.

It is needless for me to discuss in this place the histology of the tubular portion of the pronephros. These details have little general interest, and they have furthermore been accurately given by Fürbringer and Hoffmann ('86).

The dilated chamber which I have described (page 240) was also observed by Hoffmann, but he was unable to determine what portion of the system was concerned in its formation. Similar dilated chambers are likewise described by Marshall and Bles, who regard them as steps in the degeneration of the tubules. The early appearance of these dilated regions in Rana (see page 232) seems to me to render this interpretation improbable.

According to the usual account, the capsule arises as a differentiation of the connective-tissue stroma, which lies between the pronephros and the ectoderm. Duval ('82, pp. 25, 27) alone has claimed an origin from the overlying protovertebræ; but, singularly, his statement has been wholly neglected by subsequent writers. His observations on this point agree in all essential features with my own.

The glomus was discovered by Joh. Müller ('30, p. 12), but the significance of the structure was wholly problematical until Bidder ('46, p. 58) suggested its glomerular nature, which has since received general acceptance. This view has, however, been opposed by Semper ('75, pp. 439 *et seq.*), and more recently by Hoffmann ('86, pp. 572, 573). According to Goette and Fürbringer, the glomus arises as an outfolding of the splanchnopleure opposite the pronephric nephrostomes. The interior of the fold becomes occupied by mesenchymatic cells and with blood tracts, which communicate with the aorta. According to Hoffmann, the interior is largely occupied by "columns" of large cells, which would seem foreign to the nature of a glomerular structure. These 'columns of cells," he says, may be seen to arise, in Bufo at least, by the invagination of the superficial covering of the glomus. I have myself seen continuous cylindrical cords of cells in the glomus; but in most cases I have been readily able to satisfy myself that this appearance had to do with densely packed blood cells lying in a definite vascular tract. I have also occasionally met with invaginations of the superficial (peritoneal) epithelium of the glomus (page 247); but it seems to me, even should it be shown that they give rise in the interior to columns of cells, that this would not be a very serious objection to the view which ascribes to the organ a glomerular function. In favor of that view, many arguments may be adduced: (1) the highly vascular nature of the glomus; (2) its position in an open chamber of the body cavity directly opposite the pronephric nephrostomes; (3) its serial relations with the mesonephric glomeruli; (4) its appearance and degeneration synchronously with the pronephros; and (5) the circumstance that its homologue, wherever found in other classes of Vertebrates, is always in equally close relation with excretory tubules. The last argument seems to me the most weighty, and I am of opinion that a comprehensive comparative study proves beyond question the glomerular nature of the structure.

In the descriptive part of this paper I have stated that, in satisfactory sections through the blood-vessel which leads from the aorta to the glomus, one could frequently observe that the ramifications within the glomus did not appear to be terminal, but that the vessel seemed to give off a lateral branch to the glomus, while the main trunk continued on toward the ventral side of the body. An explanation of this condition has occurred to me, which, if confirmed, will be of considerable morphological significance, though at present I can merely offer it as a suggestion. As we have already seen, the glomus of Selachii, according to Rückert ('88, pp. 239–242), does not receive a separate blood-vessel directly from the aorta, but a rete mirabile is developed in connection with the segmental vessels described by Paul Mayer. I have not succeeded in tracing the main aortic branch to the ventral side of the larva; but, as far as it could be followed, the course of the vessel between splanchnopleure and entoderm corresponds perfectly with that of one of the segmental vessels described by him. It seems to me quite possible that, in Amphibia, the dorsal portion, which is in communication with the glomus, is the only part of these rudimentary vessels which is retained, and that the remaining portion, having ceased to be of functional importance, fails to develop.

Having completed my survey of our knowledge of the development of the pronephros in the several classes of Vertebrates, I now turn to a consideration of the development of the segmental duct. As is well known, observers up to a very recent date have been almost unanimous in ascribing a mesodermal origin to this structure. In regard to the details of the process, however, they have been less at one ; and I shall accordingly treat of their accounts under three heads, which seem to me to represent fairly well marked phases of opinion.

According to one view, *the duct arises as an evagination of somatopleure, its lumen being therefore a detached portion of the body cavity.* Such a mode of origin was advocated by Rosenberg ('67, pp. 42 *et seq.*) for Teleosts ; and this feature of his account has gained almost universal acceptance both for Teleosts and for Amphibia, having been recently entirely confirmed by Hoffmann ('86) and Henneguy ('88, '89). According to Wilh. Müller ('75) and Fürbringer, the duct arises in this way also in Petromyzon, and a similar claim has been made for Ganoids by Kowalewsky, Owsjannikow, and Wagner ('70), and by Balfour and Parker ('82). In Selachians, however, the weight of the evidence is distinctly opposed to this view, and I am not aware of its having been advocated by any one besides Schultz ('75).

In Amniotes also such an account of the early development has not received general acceptance ; it was first claimed in this class by Romiti ('74), and was adopted, with some modification it is true, by R. Kowalewsky ('75), and by Dansky und Kostenitsch ('80, p. 24). Very recently such a mode of origin has been reasserted by Fleischmann ('87) for Carnivores and the Duck.

My own observations on Amphibia indicate that in this group the duct does not arise as a fold ; and I am of opinion that, in both Cyclostomes and Ganoids, the evidence that the duct arises by evagination is at present unsatisfactory. It seems to me probable, on the contrary, that the method of origin which is usually recognized as characteristic of all the Anamnia with the exception of Selachii exists, if at all, only in Teleosts. In view of the peculiar obstacles which Teleostean material presents for embryological study, one should be cautious in affirming for this group a mode of development which, in my opinion, is not proved to exist in any other class of Vertebrates.

A second view of the origin of the duct is, that it *arises from a solid proliferation of somatopleure.* According to Fürbringer ('78^a), Spoof ('83, p. 84), and the earlier writers (Remak, '55, Kölliker, '61, Bornhaupt, '67, Waldeyer, '70, and Foster and Balfour, '74), the duct arises in the chick by a proliferation *in situ* of the subjacent mesoderm, and a similar origin is maintained for Petromyzon by Scott ('82). The more recent view, however, affirms that the posterior end of the duct grows backward free from adjacent tissue, the cellular material being wholly derived from an anterior proliferation. For Selachii this method of origin has been maintained by Balfour ('78), and for Amniotes by a large number of observers ; e. g. Weldon ('83) and Mihalkovics ('85) in Reptiles; Gasser ('77), Sedgwick ('81), Schmiegelow ('81 and '82), and Janošik ('85), in Birds ; Renson ('83) and Martin ('88), in Mammals. Gasser ('82) believes that the segmental duct in Alytes has no direct connection with the mesoderm, posterior to the pronephros ; but he was unable to exclude with certainty the possibility that the somatopleure immediately behind the pronephros might take some part in the formation of the duct. Mollier ('90, p. 226) moreover asserts that such a participation actually takes place in the two somites following those in which the pronephros is formed, but that the posterior portion of the duct probably grows back from this point independently of the mesoderm.

In so far as these authors maintain that the duct arises from a solid proliferation of mesoderm and acquires its lumen secondarily, I entirely agree with them ; but my observations on this point lead me to conclude further that the duct arises throughout its entire length from a continuous thickening of somatopleure, and that the only free growth which occurs in the Amphibia studied by me is for the purpose of effecting a union with the cloaca. In assuming this position, I am aware of being in conflict with prior observations on Amphibia, and with the more recent accounts of the development in other groups ; it seems to me, however, that satisfactory evidence in favor of this mode of origin has been adduced in the descriptive part of this paper.

Finally it remains for me to consider the third view, that of the ectodermal origin of the duct, which is to-day advocated on so many sides. As early as 1855 Remak expressed himself as dissatisfied with the derivation of the excretory system from the mesoderm, although this mode of origin was confirmed by his own observations. A decennium later His ('65^b, pp. 160–162) maintained that, in the Chick, the Wolffian and Müllerian ducts both arise as folds of the ectoderm ; but he abandoned this position later ('68, p. 119), when it had been shown by Bornhaupt ('67) and Dursy ('67) to be untenable. He then endeavored to interpret the facts in harmony with his theoretical conceptions by maintaining that the cells from which the Wolffian and Müllerian ducts arose were primarily derived from the ectoderm, a view which was likewise adopted by Waldeyer ('70). Meantime Hensen ('66) had indorsed the view of a direct origin from the ectoderm. He states ('66, p. 81, foot-note) that in the Rabbit the Wolffian duct arises from a solid rod-like thickening of the ectoderm near the middle protovertebræ. In a second short communication ('67, p. 502), Hensen merely reaffirmed his confirmation of His; but finally he ('75–'76, pp. 369–372) published a fuller account of his observations, accompanied with figures. These, however, are far from conclusive, and it does not seem surprising that this single observation was distrusted by subsequent writers.

In 1884 Graf Spee published an account of his very careful investigation of the subject, and reasserted the ectodermal origin of the Wolffian duct.[1] Following this publication have appeared a large number of confirmatory papers, which have moreover extended the observations of Graf Spee; so that at present the ectodermal origin of the duct has been asserted for every class of Vertebrates, with the single exception of the little known Dipnoi.

As stated in the Introduction to the present paper, it was my hope in undertaking these studies to find in Amphibia results confirmatory of Graf Spee's position. If, then, a contrary result has been reached, it has been because I have been driven to that conclusion by evidence brought out in the course of the investigation. In my opinion, the entire excretory system of the forms I have studied unquestionably develops without any participation of the ectoderm in its formation. The duct develops from mesoderm throughout its entire length, and at its posterior end, in Rana and Bufo at least, comes in contact with one of the entodermal cornua of the hind gut; so that *nowhere* in its development does it come into organic union with the outer germ layer.

I must in this case distinctly disavow the suggestion of Hertwig ('88, p. 280), who endeavors to harmonize the accounts by assuming that only the posterior end of the duct is formed from the ectoderm. This explanation would by no means be admissible, unless it be granted that the ectodermal constituent might in this case be reduced to nothing at all. On the other hand, it must be confessed that a fundamental opposition in the mode of development of an organ in two closely related groups is at present hardly reconcilable with our general conceptions of embryological processes.

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[1] Graf Spee, and subsequently Flemming ('86), did not clearly recognize the fact that the Wolffian duct and the mesonephros develop in different ways, and were led to defend an ectodermal origin for the *excretory system*. This interpretation is in evident opposition to the accounts of others, and, in my opinion, is not justified by their own observation, even should these prove to be accurate in every particular.

It will therefore be of interest to review critically the most recent accounts in the several groups, for the purpose of ascertaining whether the ectodermal origin of the segmental duct be in any case actually demonstrated. For this purpose, only those papers which have appeared since Graf Spee's researches need concern us. Of these, the larger number are brief notices, which, in view of the extreme difficulty of the investigation, cannot be regarded as conclusive.

In regard to Cyclostomes, the only papers that have appeared during this period have been preliminary notices; that of Kupffer ('88) maintains an ectodermal, those of Goette ('88) and Owsjannikow ('89) a mesodermal, origin for the duct.

In Teleosts, the duct has been claimed to be ectodermal by Brook ('87) and Ryder ('87); but on the basis of my own observations, which are as yet incomplete, I am led to doubt the correctness of this claim, which has already been opposed by the observations of Henneguy ('88), of H. V. Wilson ('90), and of McIntosh and Prince ('88). In the account by Brook, it seems to me probable that the ectodermal thickening observed has in reality a very different significance (lateral line proliferation) from that attributed to it, an opinion which is shared by Wilson ('90, p. 58). The only recent paper dealing with the development of the Ganoidean excretory system is the preliminary notice of Beard ('89) on Lepidosteus. According to Beard, the duct is ectodermal.

In Amphibia, also, an ectodermal origin of the segmental duct has been asserted by Perenyi ('87) and by Brook ('87). Their communications, however, are both short notices, and in the absence of the final papers cannot be regarded as satisfactory evidence. Moreover, the mesodermal origin of the duct has been reaffirmed by Mollier ('90), Kellogg ('90), and Marshall and Bles ('90).

It is rather remarkable, that, in all the preceding classes, nothing but preliminary notices have ever appeared in favor of the ectodermal view. The same is true of Birds, where this mode of origin has been claimed as probable by Beard ('87) and by Brook ('87). On the other hand, a number of observers have carefully investigated the chick with this special purpose in view, and have been unable to find any evidence of a participation of the ectoderm in the formation of the Wolffian duct. Among these may be mentioned Janošik ('85), Mihalkovics ('85), and Hoffmann ('89). Peculiarly significant, however, is the fact that Graf Spee ('86) was unable with the use of the most various reagents to see any direct evidence of a genetic connection between the ectoderm and the Wolffian duct in the *Chick*.

In Reptiles, a number of writers have asserted that the Wolffian duct arises from the ectoderm. According to Perenyi ('87, '88, '89), irregular groups of cells are at an early stage budded off from the ectoderm covering the middle plate, and on the first formation of the segmental vesicles they form the cord of cells which has been recognized by prior writers as the fundament of the duct. In my opinion, no conclusive evidence is adduced to prove that the cells figured in the latter position ('89, Fig. 5, *ceW.*) are descendants of those which at an early stage form part of the ectodermal thickening. Mitsukuri ('88) and Orr ('87) have published short notes claiming an ectodermal origin for the duct; and, finally, Ostroumoff ('88^a, '88^b) asserts that it is derived from the ectoderm in Phrynocephalus. It seems to me, however, that Ostroumoff's observations are incomplete at a critical point, and that no satisfactory evidence is brought forward to show that the ectodermal thickenings which he describes and figures ('88^b, Tab. III. Fig. 56) with all desirable clearness, are unquestionably the fundament of the Wolffian duct. They may be merely chance thickenings over the intersegmental depressions in the underlying mesoderm. On the other hand, Mihalkovics ('85), Strahl ('86), and Hoffmann ('89) have all sought in vain to find satisfactory evidence of a participation of the ectoderm in the formation of the Wolffian duct.

With all the preceding classes of Vertebrates, I am of opinion that the weight of evidence is at present in favor of the view that the excretory system is wholly derived from the mesoderm. For the remaining groups, Mammals and Selachians, however, no such claim can be sustained. The researches of Graf Spee on Cavia showed conclusively that a cord of cells representing the fundament of the Wolffian duct is continuous posteriorly with a ridge of tissue which is still in intimate union with the superficial ectoderm, and that, in the further development, a continuous cord of cells separates off from this ridge by the progressive formation of a split between the deep portion of the ridge and the superficial ectoderm. At first, a distinct membrana prima is reflected from the unmodified ectoderm over the ridge, and the partially separated fundament of the duct may still be in connection with the superficial ectoderm by means of such a membrane. This latter feature is also dwelt upon by Flemming ('86), who furthermore emphasizes the circumstance that in the ridge which forms the first rudiment of the Wolffian duct mitoses are especially abundant, and that the nuclear spindles are frequently perpendicular to the surface, i. e. are so situated that the ensuing cell divisions would tend to thicken the layer. The general results of these two investigators have been confirmed by Bonnet ('87 and '88) in the Dog and Sheep, and a number of former advocates of a mesodermal origin have satisfied themselves of the correctness of the opposed view by a study of the preparations of these authors; e. g. His (see Spee, '84, p. 93), Waldeyer (see Janošik, '85, p. 13), and Mihalkovics (see van Wijhe, '89, p. 501).

The most recent paper on this subject is that of H. Meyer ('90), who claims an ectodermal origin for the Wolffian duct in man. The embryo upon which these observations were made was obtained by artificial abortion, and was at once preserved by histological methods; so that, in the opinion of the author, it would be unfair to ascribe his results to imperfect preservation, which so frequently renders observations on human material untrustworthy. On the other hand, the mode in which the duct is here claimed to originate, viz. as a conspicuous *fold* of ectoderm, is so different from the method of origin described in other Mammals that one cannot regard this observation based on a single specimen as conclusive evidence.[1]

A few recent writers have reasserted the mesodermal origin of the Wolffian duct even in the case of Mammals. Lockwood ('87, p. 642) criticises the evidence adduced by Graf Spee and Flemming, and compares their ectodermal ridge to a number of insignificant ectodermal thickenings which may be observed over depressions in the underlying tissue in diverse regions of the body. Lockwood entirely ignores the very definite relations which Graf Spee showed to exist at a certain stage between the fundament of the duct present in anterior regions and the continuous posterior ridge; his entire criticism therefore seems to me quite unwarranted. Fleischmann ('87) also reasserts in a preliminary note the mesodermal origin of the duct in Carnivora; but his description of the mode of origin is so entirely at variance with the accounts of recent authorities that his statements can hardly be regarded satisfactory before the evidence on which they are based is produced.

On the other hand, Martin (Stahl und Martin, '86, Martin, '88) accepts the main features of the development as described by Graf Spee and

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[1] During the correction of these proof-sheets another paper has appeared which asserts a participation of the ectoderm in the formation of the duct in Man (Kollmann, '91). In the region of the middle plate there is found, according to this author, a close fold of ectoderm (Taf. III. Figs. 3, 4, *Anlage d. Urniere*, Fig. 8^a) which he believes to be concerned in the formation of the duct, thus confirming Meyer's ('90) account. The later stages studied by Kollmann, however, are too far advanced to afford convincing evidence that his interpretation of the fate of this fold is accurate.

Flemming, but interprets their observations in a fundamentally different way. In the course of a painstaking investigation, in which more than forty series of sections were used, Martin never encountered conditions which in his opinion demonstrated a genetic connection of the duct with the ectoderm. He believes that the duct arises from a proliferation of mesoderm in the region between the 9th and 11th protovertebræ, and grows backward by cell division within its own mass. The posterior portion of the duct, however, fuses with the ectoderm so intimately that in certain regions it is quite impossible to recognize a boundary between them; but Martin believes that the fusion is wholly secondary, and that the ectoderm contributes no material to the duct. Keibel's ('88^a, p. 635) studies on Erinaceus led him at first to accept Martin's attempt at harmonizing the two views; but in Cavia ('88^b, pp. 424–428) his observations inclined him towards the original view of Graf Spee.

In my opinion, Martin is right in denying that an ectodermal origin of the Wolffian duct has been demonstrated in Mammals. It is undoubtedly true, that there is considerable evidence in favor of such a mode of origin; but it is not of a nature that would warrant one in concluding that the duct arises in this way throughout all Vertebrates, or in asserting that it develops in fundamentally different ways in Mammals on the one hand, and in other Vertebrates on the other. All that can be claimed, however, in accordance with Martin's view, is that it is possible to interpret the conditions in Mammals in agreement with observations in other Vertebrates, should these be shown to be less ambiguous.

In Selachians, the evidence in favor of an ectodermal origin of the duct is perhaps even stronger than in Mammals. In the former group, besides the preliminary communications of van Wijhe ('86, '88^a) and Beard ('87), there have appeared two extensive papers by Rückert ('88) and van Wijhe ('89), which seem to place the ectodermal origin of the segmental duct almost beyond question; and, so far as I am aware, no recent observer has expressed doubts upon this point. It nevertheless seems to me that, before accepting this result as final, we have yet to inquire whether Martin's interpretation of the condition in Mammals cannot be applied also in Selachii.

It might be objected, that the latter view offers no explanation for the intimate fusion which must be granted to exist between the posterior end of the segmental duct and the ectoderm; yet this argument cannot invalidate the general conclusion, since a number of cases of such a union of two epithelial structures in their growth have been recorded, where no genetic connection is believed to exist. Such a conception is involved, for example, in the account — contested, it is true — given by Carius ('88) of the anterior growth of the chorda in the "Kopffortsatz" of Cavia, the chorda being in intimate fusion with the underlying entoderm; or, again, the backward growth of the Amniotic Müllerian duct in close connection both with the Wolffian duct and with the adjacent peritoneum, as described by a number of recent writers.

In conclusion, then, I am of opinion that the more primitive condition, and that shown by most Vertebrates, is the development of the segmental duct independent of connection with the ectoderm; but that in certain groups the duct enters into a secondary union with the ectoderm. The question whether the ectoderm here contributes material to the fundament of the duct can at present receive no more definite answer than that contained in the foregoing discussion.

It has frequently been asserted that the mesodermal origin of the kidneys is not in harmony with our conceptions of the derivatives of this germ layer. As early as 1855 Remak saw a fundamental opposition in the mode of development which he described for the excretory organs, and that familiar in the case of other glands. According to his view, which received very general acceptance, the kidney is a unique example of a gland whose secreting surfaces are not derived from one or other of the bounding germ layers, ectoderm and entoderm.

In my opinion, this view must now be considered inaccurate. It is doubtless true that glands are usually developed either from the ectoderm or from the entoderm; this circumstance may merely be due to their apparently being seldom needed on mesodermal surfaces. Certain special regions, however, seem to require glands. Such regions are the sexual conduits in which, besides those glands which have special functions, such as the deposition of the secondary egg membranes[1] (Ludwig), we should expect to find glands similar to those which are found in the course of other canals leading to the exterior, such, e. g., as the trachea. I shall disregard the glands which develop in the ampullæ of the vàsa deferentia, since these are derived from the Wolffian duct and consequently *may* be of ectodermal origin in Mammals, and shall take as a specific example the genital tract of the human female. It seems very certain that in Amniotes the Müllerian duct develops entirely independently of the Wolffian duct, as an evagination of the peritoneal covering of the Wolffian body. Moreover, whether we accept the view of van Ackeren ('89), that the hymen marks the region of fusion between the fused Müllerian ducts and the sinus urogenitalis, or that of Nagel ('89), who claims that the vagina is a product of the sinus urogenitalis, the boundary between the two constituents being marked by the os externum uteri, it must in either case be granted that the entire genital tract from the ostia abdominales of the oviducts to the os externum is of mesodermal origin. This entire system is lined with a continuous columnar epithelium, which is continuous below with the stratified epithelium of the portio vaginalis. In its histological characters this membrane closely resembles a typical mucous membrane, and is subject to the characteristic disorders of this form of tissue, cancer and catarrh. The Fallopian tubes are believed to be without glands;[1] in the region of the fundus and corpus, however, are numerous long tubular cœcæ which have been called uterine glands. It has not been demonstrated, however, that these structures exercise a secretory function; and they may merely serve to regenerate the mucosa cast in menstruation. In the cervical region occur glands (glandulæ Nabothi, Schleimkrypten) which are much shorter than those in the body of the uterus. These cervical glands secrete a viscous fluid of the characteristic ropy consistency of mucus, which at periods mingles with the catamenial flow,[2] and, in certain stages of pregnancy, forms a complete plug in the cervical canal. This secretion forms a dense mass on addition of alcohol; it swells conspicuously when placed in water; it stains blue with hæmatoxylin, and pink with picro-carmin; and, finally, according to Overlach ('85) its formation is attended with the same fundamental changes in the protoplasm at the distal end of the secreting cell which are familiar in the case of ordinary mucous secretion.[3] It is almost certain that the cervical glands produce true mucus. Not merely, then, does the mesoderm give rise to glands, but *it produces glands of the same nature as those found in mucous passages of ectodermal origin.*

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[1] The albumen secretion of the Hen's oviduct is a familiar example. According to Giacosa ('72) the oviducal secretion in Rana is largely composed of mucin.

A second view was that formulated by His ('65^a), according to which the ectoderm and entoderm alone are capable of giving rise to epithelial tissues. This view, which was associated with the derivation of the urogenital tract from the ectoderm, was naturally revived by Graf Spee ('84). More recent evidence, however, shows that it is only the Wolffian duct in regard to which the question of an ectodermal origin remains open; the Wolffian tubules, on the other hand, as well as the epithelia of the female sexual tract, are distinctly mesodermal. The statement that epithelia do not arise from the mesoderm is, in my opinion, either insignificant or untrue. If, avoiding genetic characters, we define epithelium so narrowly as to exclude endothelium, we must confess that, except in certain specialized regions, epithelia do not develop from the mesoderm; but the conclusion is obviously of little morphological importance. On the other hand, if we employ broad morphological characters in our definition, such a conclusion is manifestly inaccurate.

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[1] The vagina also is stated by Veith ('89) to be normally glandless.

[2] Of interest in this connection are the observations of Artemjeff ('89), who describes mucous corpuscles as a constituent element of normal lochia.

[3] Through the kindness of Dr. C. S. Minot, I have been able to try in addition a few simple chemical tests on the cervical secretions. The cervical plug from a uterus of three months' pregnancy examined by me, proved to be soluble in potassic, sodic, and calcic hydrates, and in sodic carbonate; it is precipitated by nitric acid, but redissolves in excess; in strong acetic acid, on the contrary, it appears not to redissolve. The substance gives the proteid reaction with nitric acid, but not that with cupric sulphate. It also gave the specific mucin stain with methylen blue recommended by Hoyer ('90).

The ectodermal origin of the Wolffian duct has been supposed to account for certain pathological new formations which frequently have their seat in the urogenital organs. Thus His ('65^b) saw in the mode of development which he described for the Wolffian and Müllerian ducts an explanation for the occurrence of dermoid cysts in the ovary. It must be confessed that the structure of many of these cysts suggests that they have an ectodermal origin; but their occurrence in very diverse parts of the body shows that they do not require a normal ingrowth of ectodermal cells into the region in which they arise. Thus in the dermoid cysts which are occasionally found back of the optic bulb, the translocation must be regarded as purely adventitious.[1]

The suggestion has recently been made by Sutton ('86, p. 344), that testicular and ovarian carcinomata are to be explained by the occurrence of degenerating ducts in the neighborhood of the genital ridge, and he is inclined to regard the Wolffian duct as the means of transporting ectodermal cells to this region. The weight of evidence seems to favor the view that carcinomata cannot develop without an epithelial basis (Klebs, '89, p. 771); but this fact does not compel us to seek an ectodermal source for these growths. In the case of adenomata, which also require an epithelial basis, one can see more readily the source of the proliferation; and these abound in the ovary. The germinal epithelium, in consequence of its retention of embryonic characters, seems to be well adapted to the formation of carcinomata, and, according to Birch-Hirschfeld's ('89, p. 202) enumeration, they are somewhat more frequent in the ovary than in the testis, even though the latter organ is in such intimate relations with degenerating Wolffian canals.

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[1] Many dermoids may be explained as cases of *fœtus in fœtu*, and those in the ovary may often be due to extra-uterine gestation.

The remaining portion of the present paper will be concerned with those inferences of a general nature which can be drawn from the development of the pronephros and segmental duct as traced in the preceding pages. These general conclusions naturally fall into two groups: (1) such as are of principal interest in elucidating the development of the excretory system, and (2) such as tend to throw light on the development of the Vertebrate type. Following this division, then, in our discussion, I shall consider in the present section the organogenetic conclusions; and, in concluding, deal with the phylogenetic conclusions which seem to me warrranted by our present knowledge.

In the historical review of the development of the pronephros, it proved in several groups very difficult to draw a sharp line between the pronephros and the mesonephros, and it was suggested at that point in the discussion that this difficulty is in reality a fundamental one, and one which is indicative of the true relations between these parts. The question of the serial homology of the pronephros and mesonephros, as it presents itself to the modern student, is to my mind simply this: Are we to regard these two glands as derivatives of one continuous ancestral organ, which at one time extended over all the somites now occupied by each? The answer to this question naturally must come, if at all, by a comparison of the two organs for the purpose of bringing to light their features of similarity and those of contrast. Manifestly they differ in the time of their appearance; indeed, from this circumstance the two glands were distinguished and named; it remains to consider whether they are constructed on the same or on different types.

In endeavoring to furnish an answer to this question, I shall proceed to an anatomical comparison of the glands, taking into consideration both of the principal portions involved, the glomerular and the tubular parts. The glomerulus of the mesonephros resembles the glomus of the pronephros in the following particulars: both are highly vascular structures composed of ramifying blood-vessels and mesenchyme; they project into spaces which are in communication with the exterior by means of excretory conduits; they originate outside of this space, and gain position within it by pushing before them in their growth its epithelial wall, which then persists as an outer covering to the vascular process; they receive branches directly from the aorta; and, finally, they are developed in regions of the body which at least nearly correspond to each other serially, as is shown by the relations of the glomus and the glomeruli respectively to the aorta, and by the existence of transitional glomeruli (Birds, Crocodilia, Chelonia). On the other hand, the features in which the glomus differs from the glomerulus may be summarized as follows: the glomus lies in the body cavity, instead of projecting into the lumen of a specialized excretory tubule, and it is a continuous structure, instead of consisting of a number of separate parts.

Turning now to the tubular portions of the two glands, one can recognize a number of common characters. In both can be distinguished a longitudinal conduit and transverse canals, the latter communicating with the body cavity by means of ciliated nephrostomes. The longitudinal canal of the two glands is in reality a continuous structure, the segmental duct. Since the pronephric and the mesonephric tubules are similarly related to this continuous duct, it is evident that they must themselves lie in approximately equivalent regions of the body. The metamerism of both glands primitively corresponds to that of the body somites; this feature is apparent from my account of the Amphibian pronephros, and has been proved for the most anterior mesonephric tubules in Amblystoma (see page 261), as well as for the entire series in Selachii and certain other groups. Finally, the cardinal veins give rise to a meshwork of vascular spaces which bathe in a like manner the tubules of the pronephros and mesonephros. In addition to the different ways in which their tubules are related to glomerular structures, the pronephros and mesonephros are unlike, in that the tubules of the former develop in continuity with the duct, while those of the latter join the duct secondarily. The character of the convolution also is different in the two glands. As is evident from the reconstructions (Plates IV. and VIII.) of the pronephros in Rana and Amblystoma, the complication is here mainly due to the convolution of the longitudinal canal (common trunk); whereas in the case of the mesonephros the longitudinal canal (segmental duct) traverses the gland as an almost straight duct, the transverse tubules alone being highly convoluted.

The pronephros and mesonephros, then, present many striking anatomical features of resemblance, but also differ in several respects. I am however of opinion, that the similarities of structure are sufficiently great to make it probable that pronephros and mesonephros have developed from a common beginning. I do not think, however, that such tabulation of the resemblances and differences gives an adequate insight into the true relationships of the structures. In the search for ancestral characters, it is a matter of indifference whether the organ in question actually realizes a given character, or merely shows a tendency to assume it, provided in the latter case it can be satisfactorily shown that the realization of the tendency was prevented by intelligible causes. Thus, in the gastrulation of meroblastic eggs, if it be recognized that the great accumulation of yolk renders emboly impossible, the substitution of epiboly in these cases must be regarded as morphologically insignificant.

The question now naturally arises, Are any of the contrasts between pronephros and mesonephros of such a nature that they can be explained as the result of a single modifying influence? As I have already stated, the most marked point of disagreement between the two glands is the difference in time at which they appear. What influences may that factor exert in modifying their development? At the time when the Amphibian mesonephros appears, the myotomes are widely separated from the peritoneum, and the continuous strip of cœlom immediately ventral to the lower boundaries of the protovertebræ in the region of the pronephros does not exist in the region of the body in which the mesonephros develops. In its place is a mass of cells which extends from the dorsal angle of the body cavity upward towards the overlying myotomes. This mass of cells has been regarded as the first rudiment of the mesonephros. The most natural explanation of the condition is that this mass of cells is morphologically not a secondary proliferation from the peritoneum, but is really the last remnant of the mesoderm which formerly connected the dorsal angle of the permanent body cavity with the overlying protovertebræ. The correctness of this interpretation is shown by comparison with the conditions in Selachians and in Amniotes, where, according to the mutually confirmatory accounts of Sedgwick ('80^a), Van Wijhe ('88^a, '89), Rückert ('88), and Hoffmann ('89), the mesonephric tubules develop from the communicating canal. The first rudiment of each mesonephric tubule is in reality that portion of the primitive mesodermal plate which lies immediately ventral to the protovertebræ, and, corresponds to that portion of the cœlom into which, as shown in Figure 6, the glomus projects, and from which the pronephric tubules emerge. *Each mesonephric fundament, then, presents on its outer side somatic, on its inner, splanchnic mesoderm.* When the fundaments of the mesonephros have been converted into a series of blind tubules, they grow outward and join the segmental duct. This process appears to me to be precisely equivalent to the *somatopleural* evagination, which at an early period gave rise in the anterior region to the nephrostomal tubules of the pronephros. That portion of the differentiated mesonephric tubule into which the glomerulus projects is of different origin; it is merely a portion of the cœlom, the walls of which are to be understood to be formed as I have just stated in part by somatic, in part by splanchnic mesoderm.

Returning now to the two features in which the glomus was shown to differ from the glomeruli, — viz. situation within the body cavity, and continuity throughout successive somites, — it will be seen that it is impossible to maintain the former as a ground of distinction, since the glomerulus also lies in a detached portion of the cœlom, and that the latter ground is equally untenable because it simply results from the fact that, before the glomeruli appear, the space into which they would otherwise project as a continuous organ has already been broken up into a series of distinct tubes; the glomerular organ is consequently broken up into a corresponding number of separate vascular processes, each of which becomes converted into a Malpighian capsule.

It seems probable, therefore, (1) that the pronephros and mesonephros were primitively alike, and were portions of a single continuous gland; (2) that in Vertebrates which came to lead an independent existence early in life, an anterior portion of the gland and the whole of the duct are differentiated before the posterior part for the immediate purposes of the larva; and (3) that the difference in structure between the two glands is mainly due to their arising at different times relatively to the differentiation of the body cavity and protovertebræ. Applying this conclusion to the tubular portion of the glands, it becomes at once intelligible why the tubules of the mesonephros must of necessity join the duct secondarily. From this standpoint, the existence of convolutions in the common trunk points to a less differentiated condition of the pronephros, in that, for temporary purposes, the longitudinal canal, including the common trunk, subserves at the same time the functions of an efferent duct and of a secreting tubule.

The foregoing explanation of the nature of the pronephros is based upon the assumption that it is developed as a larval excretory organ. In order to justify this position, it will be necessary to consider whether the pronephros is functional in those Vertebrates which, viewed from this standpoint, would seem to require this organ, and in such alone. For the present purpose, two methods of sexual reproduction may be distinguished: (1) that in which the mother spends her energy in producing a large number of offspring, which are early forced to care for themselves; and (2) that in which the mother produces a small number of eggs, and, either by giving to each a large quantity of reserve food yolk, or by nourishing the young embryo within her own body, secures the existence of her offspring without calling into play their individual activities. In the former class may be reckoned Cyclostomes, Teleosts, Ganoids, Dipnoi, and Amphibia.[1] Omitting from consideration the little known Dipnoi, a functional pronephros appears in all the members of this group without exception, and is most highly developed in those forms (Petromyzon, Amphibia) which pass through a protracted larval stage. The other class includes Selachians, Reptiles, Birds, and Mammals. In every member of this group the pronephros is rudimentary.

I conclude, therefore, that pronephros and mesonephros are parts of one ancestral organ; that the glomeruli are strictly homodynamous with the glomus; that the entire tubular portion of the pronephros is represented in the mesonephros; that the cavity of a Malpighian capsule and the nephrostomal canal connecting it with the body cavity are detached portions of the cœlom, the equivalents of which are not thus differentiated in the pronephros; that the pronephros is developed as a larval excretory organ; and that the period at which it appears largely accounts for its peculiarities of structure. This general conclusion, which is mainly based upon a study of the conditions in Amphibia, is, in my opinion, in perfect harmony with the recorded observations on other groups.

It must be remembered in this connection, however, that the pronephros may possibly have been developed from the primitive excretory organ independently in two or more groups, in response to similar physiological necessities. While I have not been able to preclude this possibility, I am nevertheless inclined to the opinion that in general a closer relation exists, and that consequently the pronephros is homologous throughout all Vertebrates. An interesting condition manifests itself in those forms (Teleosts and Ganoids) in which the pronephros remains functional until the individual is nearly adult. In these the pronephric chamber becomes partially (Lepidosteus) or entirely (Teleosts) cut off from the body cavity and comes to resemble an enormous Malpighian capsule. The region in Crocodilus intermediate between pronephros and mesonephros shows a similar differentiation of a part of the cœlom into a distinct excretory chamber. The condition in this region differs from that of the mesonephros of this genus solely in the circumstance that the excretory chamber is not broken up into metameric portions; this process takes place in the posterior region, and produces a typical mesonephros.

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[1] In the one group, the eggs are holoblastic, or if meroblastic contain little yolk (Teleosts); in the other, they contain much yolk, or the young are nourished by means of a placenta (Mammals). Mr. Samuel Garman has kindly called my attention to a number of cases in Amphibia where the period of larval life is greatly reduced. The occurrence of holoblastic segmentation in this group appears to me to afford adequate evidence that such conditions are secondary. Moreover, there actually appears to be a reduction of the pronephros in such species as abandon in part their larval life. In the case of Hylodes martinicensis, mentioned by Mr. Garman in this connection, Selenka ('82) has shown the pronephros to be very degenerate.

It now remains for me to review the opinions of previous writers in respect to the nature of the pronephros. The existence of a larval excretory system different from and earlier than the mesonephros appears to have been first suggested by Marcussen ('51); but this view received no recognition until it had been reasserted by Wilh. Müller ('75), who gave to the pronephros a distinctive name, *Vorniere*. Semper ('75), on the other hand, denied utterly the nephridial nature of the pronephros, and regarded the glomus as equivalent to the suprarenals (Nebennieren) of Plagiostomes. Fürbringer ('78^a) vigorously opposed this view, and maintained that the pronephros and its duct represent a primitive excretory system which conspicuously differs from both mesonephros and metanephros. According to Balfour's ('75) earlier view the segmental duct is formed by the backward growth of a single anterior evagination, which may be regarded as the representative of a mesonephric tubule. He ('81) later interpreted the pronephros similarly to Fürbringer, but was still inclined to believe that each mesonephric tubule was "in a sort of way serially homologous with the primitive pronephros." It is very difficult for me to reconcile the latter opinion with his view that the pronephros is a primitive excretory system derived from Plathelminthes, while the mesonephros is a secondary (new) development which does not appear until the trunk becomes segmented. Moreover, this view manifestly ignores the metamerism which is exhibited by the pronephros. It appears to me therefore entirely unsatisfactory.

Sedgwick ('81) first distinctly stated the conclusion that the pronephros and mesonephros are differentiations of a single ancestral organ. This view, which was adopted by Renson ('83), does not seem to have been generally accepted, although several authors, by describing what they denominate a transitional region, seem to me implicitly to assume an intimate connection between the two glands. Mihalkovics ('85, pp. 65, 66) denied that they are *wholly* homologous, on the ground that the pronephric tubules are peritoneal evaginations, whereas those of the mesonephros are differentiated in the solid Wolffian blastema. Mihalkovics does not explain *his* use of the term *complete* homology, and I have been unable to satisfy myself in regard to the precise relations which he supposed to exist between the two glands.

Van Wijhe ('88[a], '89), Rückert ('88), Hoffmann ('89), and Wiedersheim ('90), have distinctly denied the serial homology of the pronephros and the mesonephros. The objections of these authors to the view which I have adopted have been most clearly formulated by van Wijhe ('89, pp. 509, 510), whose account I shall follow in my criticism of their position. First, "the pronephros arises before the appearance of the duct or the mesonephros, and is indeed the first part of the excretory system that appears." This point of difference is, as I have stated, the most conspicuous feature in which the two glands are unlike. It is, however, not a weighty argument against their serial homology. Secondly, "the pronephros arises as an (in Selachii segmented) evagination of the somatopleure; its cavity, which may be temporarily obliterated by the proliferation of the walls, is formed as an evagination of the body cavity (Metacölom). The mesonephros, on the other hand, is not formed as an evagination, and it is constituted of somatopleure as well as of splanchnopleure." This analysis seems at first sight to establish a fundamental contrast between the pronephros and the mesonephros, and I admit fully the cogency of the argument in disproving a comparison of the nephrostomal and glomerular portions of a mesonephric tubule with the nephrostomal canal of the pronephros. On the other hand, however, I would insist that a hitherto unnoticed homologue of the pronephric evaginations is to be found in the *outward growth* of the primitive mesonephric canal to join the duct.[1] (See page 301.) It is in precisely this way that a tendency to a somatopleural evagination would of necessity manifest itself. Thirdly, "the duct always appears in continuity with the pronephros, but always discontinuous with the mesonephros, which only secondarily fuses with it and empties into it." This circumstance, as I have already shown, is a direct consequence of the condition explained under the first head. Fourthly, "the mesonephros possesses Malpighian corpuscles; while the pronephros has none, the glomus of the latter not being homodynamous with the glomeruli of the mesonephros because it is a vascular tuft invaginated into the secondary body cavity (Metacölom)." This contrast appears to me morphologically inaccurate, as I believe I have adequately shown in the preceding discussion.

A further objection, which van Wijhe does not mention in his enumeration, is the occurrence of rudimentary mesonephric tubules in the somites which formerly gave rise to the pronephros. To prove this assertion, it is usually regarded adequate to show the existence in the pronephric region of metameric diverticula proceeding from the body cavity towards the overlying protovertebræ. These diverticula are the communicating canals, and it is undoubtedly true that from similar canals in the posterior region mesonephric tubules are actually developed; but, to my mind, the occurrence of these diverticula in the pronephric region cannot be brought forward as evidence of the existence of two sets of nephridial tubules in these somites, until it can be shown that these remnants of the canal-like communication between protovertebræ and lateral plates exhibit some indication of the characteristic nephridial differentiation. i. e. grow outward and join the duct. This, I believe, has never been *demonstrated.* The existence of such a growth has, however, been asserted by several observers; but it seems to me compatible with the view I have expressed of the relations between pronephros and mesonephros. Since the time of the investigations of Balfour and of Semper on Selachians, it has been a familiar fact, that, although at first only one mesonephric tubule occurs in each somite, the further complication of the gland is largely produced by the formation of new tubules which proceed from the region of the primary Malpighian capsule. If the development of more than one tubule in a somite became normal in the ancestors of the Craniotes before the separation of pronephros and mesonephros took place, the development of such secondary tubules in the pronephric region would at once be intelligible.

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[1] This is the only portion of the mesonephric tubule which can properly be called an evagination; the entire tubule comprises the evagination plus the communicating canal.

A more fundamental objection is contained in an ignored observation of Gasser ('82, p. 96) on Alytes, according to which a typical glomus is developed in the body cavity of the mesonephric region, in addition to the universally present glomeruli. Gasser's account is contained in a rather short note unaccompanied by figures; it has not been confirmed by any subsequent observer; nor have I been able to find such a structure in either Rana or Amblystoma. I am therefore inclined to the opinion that Gasser may have mistaken for the glomus either the germinal ridge or the fat-body, both of which are developed in this region, although this explanation would contradict the statement of Gasser that the mesonephric glomus is a transitory organ. Be that as it may, I cannot without further evidence accept his account as final.

Semon ('90) has recently asserted that the pronephros and mesonephros are built upon the same structural type. He was led to this conclusion by a study of the excretory system in Ichthyophis. I have already alluded to the condition of the pronephros in this form. It is characterized by the possession of a completely closed pronephric chamber, from which a portion of the nephrostomes ("inner" nephrostomes) emerge. Each nephrostomal canal, however near the nephrostomal end, is joined by a branch which communicates with the permanent body cavity by means of an "outer" nephrostome. According to Semon, the pronephric chamber, as well as the cavity of a mesonephric Malpighian capsule, is a diverticulum of the cœlom; and the nephrostomal canal which joins the glomerular portion of a mesonephric tubule with the body cavity is represented by those canals of the pronephros which emerge from the open body cavity. The mesonephros is to be regarded as a "generation" of excretory tubules younger than the pronephros, and the latter may be conceived to have primitively extended throughout the entire trunk. In many features Semon's view is similar to that expressed in the preceding pages. The point of difference which I would here emphasize is the different way in which the nephrostomal canal of the mesonephros is explained. According to my opinion, *this canal is a remnant of the communication between the protovertebral cavity and the secondary body cavity, and is not represented in the tubular portion of the pronephros.* Semon, on the other hand, claims that it is the homologue of the outer series of nephrostomal canals in the pronephros of Ichthyophis. Considering the relations of the glands in that form alone, this view seems well justified; but it neglects the significant relation which has recently been shown to exist between the mesonephros and the communicating canal; and I am of opinion that the view as applied to other Vertebrates is untenable, unless it can be shown that the outer nephrostomal tubule of the Gymnophionian pronephros also develops from that canal. The latter interpretation is, I must admit, at least possible; but we must await further researches on the development of these Amphibia before accepting such a conclusion.

The closing section of this discussion will be devoted to a consideration of the evidence which the development of the excretory system as a whole throws on the origin of Vertebrates.

Two methods of investigation, which are mutually dependent, yet quite unlike in their application, may be employed in attempting to draw phylogenetic conclusions. One of these methods is peculiar to embryological research; it is dependent upon the principle that ontogeny is in part an abbreviated recapitulation of phylogeny; its method is to eliminate cœnogenetic characters; it accomplishes this largely by the aid of a physiological estimate of the influences of larval and embryonic environment, and it is comparative only throughout the extent of the group whose origin is sought. The other method is common both to comparative embryology and to comparative anatomy; it is dependent upon the inherent improbability of the same physiological requirements, being met by the same structural device in two groups which are not genetically related; it can employ equally well, though with a somewhat different significance, both cœnogenetic and palingenetic characters; it is purely anatomical in its method, and it is in the broadest sense comparative. The first I may designate as the method of elimination, or the intensive method; the latter as the comparative, or extensive method.

I have been led to make the preceding analysis in order to employ the division thus indicated in the subsequent discussion, and also because it is a contrast which does not appear to be generally recognized. Thus, a recent text-book of zoölogy (Hatschek, '88, pp. 25, 26) identifies the methods of embryology with those of comparative anatomy, and declares that palingenetic and cœnogenetic characters are equally valuable for phylogenetic inferences. According to the preceding analysis, these two statements are partial, relating only to the comparative method in embryology, and ignore the higher use which renders embryological facts of peculiar value.

Observing then this two-fold division in the following discussion, an attempt will first be made to reconstruct from the ontogeny of Vertebrates the ancestral history of their excretory organs.

The most general character which appears to be common to the ontogeny of all Vertebrates is the intimate relation which exists between the excretory tubules and the cœlom. This relation is peculiarly well illustrated by the pronephros, but it is true also of all the urogenital organs, and is a fact which in my opinion throws considerable light on their evolution. The cœlom appears to be an internal cavity developed to meet a number of physiological needs. It is likely that in the lower Invertebrates the cœlom served largely a nutritive function (see, e. g., Chun, '80, pp. 248–253); but I am of opinion that in the higher Invertebrates and in Vertebrates the cœlom early became in large measure an excretory space. This function of the cœlom, inferred from its relations with nephridia, is in accord with its situation in the body. Evidently the organs which would be most in need of a near place of discharge for nitrogenous waste products are those which are in the highest degree metabolic. Such are, *par excellence*, the muscle masses of the body, and it is a familiar circumstance that in all Chordates the primitive muscle plates develop from the lining wall of the dorsal segmented portion of the cœlom. It is very probable that this arrangement represents the earliest differentiation of a special excretory surface of which evidence is preserved in the ontogeny of Vertebrates.

The next step in the specialization of the urinary organs is the establishment of definite conduits for the purpose of conveying the excreted products to the outside. It is possible that simple apertures, such as the abdominal pores, at first served this end ; or, if the enterocœlous condition represent a phylogenetic stage, communications with the intestinal tube may have afforded an outlet to the excreted fluids. Be this as it may, it is evident that the ancestors of our present Vertebrates early acquired specialized tubes subserving this purpose.

In the account of the development of the Amphibian pronephros and duct given in the first section of the present paper, emphasis was laid upon the fact that these structures are differentiated from a solid somatopleural thickening, and do not arise as a fold of the peritoneum. Manifestly the former condition is cœnogenetic ; such a solid thickening could in no wise function as an excretory conduit. On the other hand, it must not be rashly assumed that the somatopleural thickening is a disguised *fold* of that layer. On the contrary, the pronephros, on canalization, shows itself to be already composed of a series of metameric evaginations of the cœlom, and it is perfectly conceivable that the pronephric thickening is a modification from a condition where the separate evaginations had their *independent* means of communication with the exterior, the several diverticula being fused into a solid mass. Either interpretation would be physiologically intelligible. In the first case, a certain region of the peritoneum would first sink as a groove into the parietes of the cœlom. This channel might, like the nephrostomes, be provided with vibratile cilia, and might thus serve to carry the fluids lodged in it back to a single pair of orifices situated near the posterior end of the cœlom. As a further differentiation, it is to be conceived that this groove became at intervals constricted off from the cœlom, forming a retroperitoneal duct with a series of nephrostomal tubules.

According to the second alternative, it is necessary to suppose that the several evaginations communicated distally either directly with the exterior or with an independent longitudinal duct. The nephridia of Heteromastus and Capitella (Eisig, '88, pp. 242, 272), in which no external opening is present, show us that the gradational steps in the formation of such outgrowths may be conceived to be functional.

In judging between the two views to which allusion has just been made, it is important to consider whether the ontogeny of other groups ever presents either of these processes in an unambiguous manner. I have already expressed my doubts in regard to the development of the pronephros and duct by the incomplete closure of a groove of somatopleure. The best attested claim that has been made for such a mode of origin was that made by Goette, Fürbringer, Hoffmann, and Marshall and Bles, for Amphibia; but this position is distinctly contradicted by my own observations. Indeed, this mode of origin has been recently denied in the case of every class except Teleosts, a group in which it is very difficult to obtain accurate evidence respecting the early history of the mesoderm.

On the other hand, numerous recent investigators have described the first rudiment of the pronephros as a series of distinct evaginations. Such observations have been recorded in Cyclostomes by Kupffer ('88), in Ganoids by Beard ('89), and in Amniotes by almost all writers on their early development. It seems to me, therefore, that the mode of formation by means of serial evaginations has a far wider distribution, and is more clearly attested, than that by means of an incompletely closed fold. I am of opinion that the condition in Amphibia and Selachia is to be regarded as derived from such evaginations by means of cœnogenetic modification; and that the weight of internal evidence is in favor of the view that the tubules were primitively distinct.

Typically the nephridial tubes are strictly metameric, one pair of tubules being developed in each metamere. The occurrence of several nephridia in a somite occurs, as we have seen, in the case of the mesonephros of certain Amphibia. This condition seems to me to be a character secondarily acquired. The following reasons confirm this opinion: (1.) In other forms, the strict metamerism of the nephridia is the earliest ontogenetic condition, the duplication of the tubules appearing much later. (2.) The dysmetameric arrangement seems to be correlated with the limited number of somites which are, in such cases, involved in the formation of the mesonephros; thus, in the Anura, a group in which the number of trunk somites is extremely small, the mesonephros departs most widely from the metameric condition; in Urodeles, the number of somites is larger, and there is an indication of metamerism in the anterior tubules; and again in Cœcilia, where the number of somites is still larger, the mesonephros has the typical metameric arrangement. (3.) The pronephros, which in general represents the least modified portion of the excretory system, retains a metameric condition in those forms in which this arrangement is absent in the mesonephros.

In order to ascertain the probable mode in which the metameric diverticula primitively terminated, whether they opened on the surface or joined a longitudinal duct, it will be necessary to consider the pronephros alone, since the segmental duct is already present before the mesonephros is formed, and we cannot expect to find an adequate criterion for determining whether the union of the mesonephric tubes with the duct be primitive or secondary. In the pronephros there is in most cases no evidence of a mode of termination more primitive than that of communicating with a duct. Two arguments, however, occur to me, which seem to indicate that a series of direct outlets to the exterior may have been early present. In the first place, the pronephric diverticula have frequently been observed to enter into intimate union with the ectoderm. Thus Rückert ('88, p. 217) was led to believe that the pronephric thickening of Selachians even received a contribution of cells from the outer germ layer. The most natural explanation of this condition seems to me to be, that the fusion of the diverticula with the ectoderm is the recapitulation in the ontogeny of a phylogenetic stage, which possessed nephridia provided with direct openings to the exterior. Secondly, Amphioxus, according to the most recent investigations, is provided with a series of nephridia opening into the atrial chamber, which latter we are, in my opinion, justified in regarding as a simple infolded portion of the exterior. Accepting the homology of the nephridia of Amphioxus and those of Craniotes, it seems to me probable that the ancestors of Vertebrates possessed nephridia which resembled those of Amphioxus in opening directly to the exterior.

If separate diverticula leading from the cœlom to the exterior be the primitive condition of the Vertebrate excretory organs, we have still to seek the origin of the segmental duct. On this point, the pronephros alone can afford evidence. The participation of the ectoderm maintained by many authors for the posterior end of the duct affords the suggestion that it may have first been formed as a groove of that layer, or that a primitive anterior opening was gradually shifted back to the cloaca. It may be objected to this view, (1) that in many Vertebrates no participation of the ectoderm occurs, while in none has it been shown that the mesoderm does not play a part in the formation of both anterior and posterior portions of the duct; and (2) that the longitudinal canal of the pronephros, which forms the anterior prolongation of the duct, in no case arises in this way. In the pronephros the longitudinal canal arises, as testified by a large number of recent investigators for divers groups, and as confirmed by my own observations on Amphibia, by the fusion of the distal ends of the pronephric diverticula. This mode of development seems to me entirely in harmony with physiological requirements; and in this earliest fragment of the excretory system we have, in my opinion, a remnant of the primitive mode of formation of the segmental duct.

The question at once arises whether there is any indication of this mode of origin preserved in the development of the posterior portion of the duct. A free backward growth, such as is maintained for many Vertebrates, is evidently far removed from the primitive mode of formation, and is to be regarded as an adaptation to the needs of the pronephros. The origin of the duct *in situ* from a somatopleural proliferation is without doubt a modified condition; yet it suggests a mode of origin which is in agreement with that observed in the anterior region. I have already emphasized the circumstance that in Amphibia the duct arises from a mass of cells which is perfectly continuous with that from which the pronephric tubules are differentiated; and it is possible that both regions represent disguised nephridial evaginations of which those in the posterior region are never differentiated as actual canals except in such portions as are converted into the duct. Further evidence in favor of this view is afforded by the occasional occurrence of supernumerary pronephric tubules such as have been observed by Mollier ('90, p. 224) and myself (page 253). The acceptance of this interpretation would necessitate a modification of our conception of the relations between pronephros and mesonephros, since we should be obliged to regard the mesonephric tubules as a second generation of tubules, the first generation having been employed in giving rise to the duct. On the other hand, it is quite possible that the entire backward growth of the duct is a *wholly* secondary process to meet the needs of a prematurely developed portion of the primitive excretory organ. This is the only interpretation which seems admissible in those cases where the duct has been found to grow backward free from adjacent tissue.

The conception of the phylogeny of the duct which I have just presented offers a partial explanation of the contradictory evidence which has been advanced respecting the germ layer from which the duct arises. With a narrower conception of the phylogeny of the duct, it is difficult to understand why the ectoderm should participate in the formation of the excretory system in one group, but not in another, and why the posterior end of the duct should in some cases be formed at the expense of a germinal layer different from that which gives rise to its anterior portion and to the nephrostomal canals wherever they appear. If, however, we assume the existence of a phylogenetic stage in which a series of nephridia open directly to the exterior, it is at once evident that a very trifling difference of location would determine whether the longitudinal canal, by means of which the duct arises, should develop from the mesoderm or from the ectoderm. It is to be remarked, however, that such an explanation is not wholly satisfactory, since one would expect on this hypothesis that those forms in which the ectodermal origin of the duct seems well attested would show evidence of close genetic relationship, while those classes in which the duct arises from the mesoderm ought to form an equally well defined group. This condition, however, is by no means realized. On the other hand, the force of this objection is materially weakened if we regard the duct as a recent acquisition, which its absence in Amphioxus gives some justification for assuming. The explanation seems to me, nevertheless, in a measure unsatisfactory, and I have adduced it merely as a possible solution of the problem to which the apparently diverse relations of the duct to the germ layers gives rise.

An intimate relation is always very early established between the excretory tubules and the cardinal veins. Such an arrangement is so favorable for the process of secretion that there can be but little doubt that this condition prevailed in the ancestors of all Vertebrates. There does not appear to be any evidence which would indicate whether the cardinal veins or the excretory tubules are the more primitive structures.

In addition to the means of excretion afforded by the epithelial walls of the tubules, the Vertebrate kidney-organs possess peculiar glomerular structures. These, as I have already shown, are all formed on the type of the pronephric glomus. In their primitive condition, they consist of vascular tufts, which receive blood from the aorta and project into the body cavity from the root of the mesentery.[1] The origin of such a primitive glomerular structure is not far to seek. It is readily conceivable that fluid may at first have simply exuded from the aorta, and, traversing the small amount of tissue intervening between it and the body cavity, may have reached the orifices of the excretory tubes prior to the development of any specialized organ subserving a glomerular function. This process being once established, any modification of structure which should allow a portion of the aortic current to be brought into closer relations with the excretory tubules would be of obvious utility, and would be preserved.

The excretory system thus constituted would represent the proneph-

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[1] The view of the excretory system here presented explains the double blood supply of the kidneys of lower Vertebrates, and also the circumstance that the Malpighian bodies always receive their blood by a direct branch from the aorta.

ric type of structure. I have already sketched the manner in which the mesonephros may be derived from the pronephros by supposing the metameric segmentation of the body to extend to that portion of the cœlom from which the nephrostomes emerge. The account given in the preceding section of this paper regarded the tubules as passive in such a metamorphosis. It is possible, however, that the transference of the tubules to a segmented portion of the cœlom may have been in part effected by a dorsalward shifting of the nephrostomes. In either case, I am of opinion that the mode of development which I have now suggested is applicable alike to the pronephros and the mesonephros, and I may also add to the metanephros (see Sedgwick, '80).

I have now presented, in a suggestive manner rather than as a complete argument, certain indications of the phylogeny of the excretory system which may be obtained from internal evidence. It still remains for us to consider what conclusions are justified by a comparative study of the excretory system, and whether the phylogenetic stages suggested in the foregoing account are to be found in any group of living animals.

The sole purpose of this discussion is to ascertain the most probable phylogenetic line of development for the excretory system of Vertebrates. For this reason, I shall avoid any discussion, which would necessarily be lengthy, respecting the interrelationships of the diverse excretory organs found in Invertebrates, simply endeavoring to seek out those classes which possess nephridia similar to those of Vertebrates, and shall ignore the further consequences which would follow from the assumption of a homology in any single case.

In the preceding account, I have provisionally accepted the view that Amphioxus belongs to the Vertebrate phylum, and have endeavored to interpret its kidneys in accordance with that view. With Tunicates it is quite different; not merely do they afford no assistance in the solution of the problem in hand, but it has hitherto proved impossible to find any organs in this group which can be regarded as homologous to Vertebrate nephridia.[1] In my opinion, it cannot be objected that the absence of such organs in Tunicates proves that the Vertebrate nephridia arose within the Vertebrate phylum. A rigid adherence to such a system of restriction in the case of other organs would quickly lead to absurd conclusions.

The only classes of animals in which we need seek for a homology of the Vertebrate renal organs are those belonging to the bilateral cladus; and among these I shall consider only those forms which are usually included in the rather heterogeneous class Vermes. This restriction is justified by the circumstance that the only similarities of structure which are to be found between the excretory system of Vertebrates and those of Mollusks and Arthropods recur with greater force in the case of several groups of Vermes.

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[1] Hatschek ('84, p. 519) regarded the single nephridium described by him in Amphioxus homologous with the neural gland of Tunicates; but I have already pointed out the probable inaccuracy of this observation.

In comparing the kidneys of Vertebrates and those of Worms, I shall distinguish three types of structure in the latter group: (1) the water-vascular system of Plathelminthes, (2) the excretory system of Nemertines, and (3) the nephridia of Annelids. The various organs which serve as excretory and genital passages in Rotifers, Nematodes, Echiurids, and Sipunculids are either referable to one of these types, or are valueless for the purpose in hand.

In endeavoring to find what points of similarity exist between the excretory system of Plathelminthes and that of Vertebrates, I have been unable to formulate any more definite statement than that both consist of longitudinal internal canals, which bear numerous lateral branches, and which open directly or indirectly to the exterior. On the contrary, the two sets of organs appear to me to perform the function of excretion by anatomical devices which are diametrically opposed. In Vertebrates, the excretions are either (primitively) poured into the cœlom and conveyed thence by a simple series of conduits, or excreted from the blood in the course of the tubuli uriniferi of the kidneys. In Plathelminthes, on the other hand, the excretory tubes ramify throughout the entire body parenchyme, and, so to speak, seek out the waste products of metabolism at the seat of their formation. It is a contrast such as exists between lungs and tracheæ, and appears to me of fundamental importance. According to Fraipont ('80) and Francotte ('81 and '83, pp. 734, 735), it is true, there is a communication between the excretory tubules of Plathelminthes and certain interior canalicular spaces, which they interpret as a rudimentary cœlom. The evidence in favor of the latter interpretation is certainly far from complete, but could not, if true, overthrow the fundamental contrast which I have just emphasized. Furthermore, I am not aware that any subsequent writers have confirmed this account of the termination of the excretory capillaries; while Pintner ('80, p. 302), von Graff ('82^a, pp. 106 *et seq.*, '82^b, p. 80), Lang ('81, p. 208, '84, p. 167), Iijima ('84, p. 400), Zschokke ('87, p. 165), and Böhmig ('90, p. 243) have all asserted that the terminal sacs are entirely closed. The conclusion seems warranted that no direct evidence in support of an intimate relation between Vertebrates and Plathelminthes is afforded by a comparison of their excretory organs.

In Nemertines the excretory system is in peculiar relations with the blood vascular system. According to Oudemans ('85), the excretory system of the Schizonemertini and the Hoplomertini consists of a longitudinal tube, which is closely applied to the lateral longitudinal blood-vessel of the œsophageal region, and this tube communicates with the exterior by means of a single excretory pore or by a number of such openings. In Carinella and Carinoma, however, the connection is much more intimate, and the glandular portion of the excretory organ lies embedded in the œsophageal blood lacunæ and communicates with the latter by means of two or three evident openings. Oudemans asserts, indeed, that the excretory system is in reality a detached portion of the blood vascular system. Bürger ('90, p. 92), however, has recently thrown some doubt upon the existence of open communications between the nephridia and the blood-vessels, but reaffirms the close dependence of the excretory system upon the vascular trunks.

Comparing the nephridia of Nemertines with those of Vertebrates, it seems to me that one cannot fail to recognize a pronounced difference in type. In Vertebrates the nephridia are canals in close relation with the cœlom; they develop from its epithelium, and even in the adult arise from chambers which must be regarded as detached portions of the cœlom. The excretory organs of Nemertines lie between the vascular trunks and the exterior, and show no such relations with the cœlom.

Among the Annelids, on the other hand, the Chætopods possess an excretory system which seems to present several features of strong resemblance with the nephridia of Vertebrates, and it remains to be considered whether an actual homology can be postulated in this case.

The points of similarity may for the present purpose be classed under seven heads. (1.) The Vertebrate and the Chætopod excretory systems agree in the fact that both primitively serve, at least in part, to convey to the exterior such fluids as accumulate in the cœlom, this cavity being used as a capacious excretory reservoir. (2.) In both groups certain portions of the epithelial lining of the cœlom become differentiated into specialized excretory glands. In Vertebrates the only structures of this character are the glomi and glomeruli; but in Annelids there is evidence that considerable areas of the peritoneum may become modified in this way. It was suggested by Claparède ('69, p. 615), that the chloragogen cells secrete certain elements from the blood and transfer them to the perivisceral fluid. This view of the function of the chloragogen cells has been confirmed by a large number of observers,[1] and it has been further shown that individual cells, having become charged with excreted concrements, loosen from the layer to which they belong, and float freely in the cœlom, whence they are discharged through the nephridia. The chloragogen layer covering the blood-vessels appears moreover from its anatomical relations to be a portion of the visceral mesoderm, and it has been shown to arise ontogenetically from that layer (Roule, '89, pp. 201, 252, 290). The chloragogen cells are frequently distributed upon special vascular processes, thus forming distinct glandular organs. Similar in function is probably the glandular envelope of the ventral vessel in Polyophthalamus (E. Meyer, '82, p. 816), and cases may be found among Polychætes in which definite peritoneal glands are present (Grobben, '88, pp. 255 *et seq.*, Eisig, '87, pp. 227, 245, 681). I should not wish to assert a strict homology between the glomus and the masses of chloragogen cells; yet it seems to me likely that the latter represent an early differentiation of the splanchnic mesoderm of which we have more specialized developments both in Annelids and in Vertebrates.[2] (3.) The efferent conduits take their origin from the cœlom by means of a series of ciliated funnel-shaped openings, the nephrostomes. (4.) The nephrostomes lead into transverse convoluted canals, along the course of which a large part of the excretion takes place. (5.) The nephridial tubes arise from the parietal peritoneum. (6.) They are typically strictly metameric, one pair of tubules being developed in each metamere. The deviation from this typical metamerism to which I have already referred in the case of Vertebrates is paralleled by similar conditions in Capitella (Eisig, '87, p. 594). (7.) The development of the Chætopod nephridia resembles in general that shown by those of Vertebrates. Both the pronephric and mesonephric tubules arise as a series of metameric outgrowths from the somatic mesoderm. In Polychætes this is evidently the mode of origin of the nephridia. In Oligochætes the development is more doubtful, but the method of origin described by Bergh ('90) is in essence the same as that known in Polychætes, and the mode of development maintained by Wilson ('87, pp. 185, 186, and '89, pp. 419 *et seq.*) may be interpreted so as not to be in fundamental opposition with such a method.

There is one feature in regard to which the nephridia of most Annelids and those of Vertebrates differ conspicuously, viz. in the mode in which the nephridia terminate. It is a familiar fact, that in Annelids each nephridium opens separately on the surface of the body; while in Vertebrates the nephrostomal tubules all connect with a pair of longitudinal ducts opening into the cloaca. In commenting upon this feature of difference, it is important to note in the first place that the contrast is not of universal application. It has been recently shown by E. Meyer ('87, pp. 618–625) and Cunningham ('87^a, 87^b, pp. 248–253) that in Lanice conchilega, a terebelloid Annelid, certain nephridia open into a longitudinal trunk, and only secondarily communicate with the exterior. On the other hand, it is probable that Amphioxus possesses nephridia which open to the exterior (atria cavity) without the intervention of a longitudinal duct. If such differences can occur among the members of either group, it seems to me that it would be unjust to deny the homology of the other portions of the system in consequence of the fact that Vertebrates *in general* possess a longitudinal duct, while Annelids *in general* do not. It appears to me, moreover, that the condition of the nephridia in Lanice conchilega and the ontogeny of Vertebrates both serve to indicate the manner in which the duct may have secondarily arisen. In Lanice conchilega there is no doubt that the nephridial duct is a secondary growth, and it is highly probable that the channel is formed by outgrowths extending from each of the nephridial tubes backward and communicating with the next following nephridium. Two groups of nephridia can be distinguished in Lanice conchilega. The more anterior of these consists of a short longitudinal duct which bears three nephrostomal tubules, and terminates at its posterior end by a single pore. In the posterior set, the longitudinal duct is merely a canal which connects the several nephridia, while these continue to retain their external orifices. I have already pointed out that the ontogeny of Vertebrates presents a similar process in the development of the longitudinal canal of the pronephros, and have shown that such changes may likewise have taken place in the region of the mesonephros. I by no means wish to imply by this comparison a belief that the ordinary mode of development in Vertebrates is to be directly derived from that presented by Lanice conchilega, nor to assume a close genetic relation between Vertebrates and genera presenting this condition. I merely wished to emphasize the fact, that in Lanice conchilega we have an instance of a species which, primitively possessing discrete nephridia, such as may have been present in the ancestor of Vertebrates, has acquired a longitudinal excretory canal by a process of transforma-

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[1] E. g. Timm ('83, pp. 122, 123); Kükenthal ('85, p. 336); Meyer ('87, p. 648).

[2] A further analogy is possibly to be found in the fact that in Amphibia certain cells early loosen from the wall of glomus and fall into the cœlom, leaving intervals between the remaining cells of the epithelium.

tion which resembles that by which Vertebrates acquire in their ontogeny the segmental duct.

From the facts thus far brought forward, I conclude, (1) that the group of animals which presents nephridia most closely resembling those of Vertebrates is unquestionably that of the Chætopod Annelids; and (2) that the Vertebrate excretory system can be readily derived from that of Annelids by a series of steps which are in accord with the evidence afforded by the ontogeny of Vertebrates.

In conclusion, I shall briefly allude to the opinions of previous writers respecting the origin of the Vertebrate excretory organs. These opinions fall, in the first place, into two classes, according to one of which the excretory system is derived from Invertebrate ancestors; according to the other, it has arisen wholly within the Vertebrate phylum.

The most recent exponent of the latter view is van Wijhe ('89, pp. 506 *et seq.*). The arguments offered by this author in support of his position are in part dependent upon his denial of the serial homology of pronephros and mesonephros. Van Wijhe also employs two arguments which are independent of his position in regard to this point: (1) nephridia are absent in Amphioxus, and therefore the common ancestral form cannot have possessed them; (2) the renal organs do not appear until after the so-called "Acrania stage," and therefore could not have appeared phylogenetically until this stage had been passed. Granting both premises, it seems to me that neither conclusion follows. With reference to the absence of kidneys in Amphioxus, the possibility — or should I not say probability? — of extensive degenerative modification is entirely neglected. Moreover, it has now been rendered probable that true nephridia do exist in Amphioxus, an observation which removes at a blow the whole basis of the argument. I do not believe many embryologists would unite with van Wijhe in holding that characters which appear simultaneously in the ontogeny of a form must necessarily have arisen contemporaneously in its ontogeny. For my part, I am unable to diagnose with accuracy the "Acrania stage" of Amphibia; but Ostroumoff ('88, pp. 77, 78) appears to have had the necessary insight, and denies emphatically that the pronephros in the case of Reptiles arises after the "Acrania stage."

Turning now to the hypotheses that have been advanced involving the derivation of the Vertebrate excretory system from Invertebrate ancestors, Haeckel ('74, p. 37), Gegenbaur ('78, p. 628), and Fürbringer ('78^a, pp. 95 *et seq.*) endeavored to show that the Vertebrate nephridia were derived from those of Plathelminthes. Semper and Balfour, on the other hand, claimed that the transverse tubules of the mesonephros are homologous with the segmental tubes of Annelids, an opinion which is shared by Beard, Haddon, Kollmann ('82^a) and others.

Rückert ('88, p. 262) has recently denied this homology, and asserted that the Annelidan nephridia are represented in the pronephros alone, since the latter is the only portion of the system of metameric tubes which comes in contact with the ectoderm. With Rückert, I would admit that the evidences of an Annelidan origin of the excretory system are to be sought mainly in the pronephros; but, in view of the intimate relations which exist between pronephros and mesonephros, it seems to me more probable that both have had the same phylogenetic origin. Ostroumoff ('88, pp. 80 *et seq.*) also has asserted that the development of the pronephros indicated that this system had been inherited from Annelidan ancestors.

On the other hand, a number of authors maintain that, although the mesonephros may be derived from the segmental organs of Annelids, the pronephric system is represented by other Invertebrate nephridia. Thus, Semper ('76, pp. 387, 388) suggests the possibility that the duct (pronephric system so far as present in Selachians [1]) may represent the unsegmented excretory tubules developed in the larva of Nephelis, or may even represent an inheritance from the Plathelminthan water-vascular system; and Balfour ('81, p. 607) was led to accept this view.

In addition to his hypothesis of an origin of the excretory system of Vertebrates from that of Plathelminthes, Fürbringer suggests the possibility that the entire system may have arisen from Gephyreans, in which unsegmented and segmented excretory organs are stated to coexist. This view was adopted by Kollmann ('82^a), and is offered as a suggestion in Wiedersheim's ('86, p. 731) text-book.

None of the views which claim a *double* origin for the excretory system seem to me to be tenable, in consequence of the fact that the pronephros, an undoubtedly segmented element, develops in *strict continuity* with the duct, the so-called unsegmented element. The view according to which the excretory system is derived from that of Gephyreans, moreover, is liable to special criticism. This claim that Gephyreans present an excretory system of a double nature, segmented and unsegmented, doubtless refers to the coexistence of two or three pairs of nephridia, together with the so-called Analschläuche of Echiurids. I am unable to see the slightest evidence that the Vertebrate excretory system is made up of such remote parts; and the hypothesis must fall to the ground as soon as it is proved that the Analschläuche are in reality only modified nephridia opening into a proctodæum. In addition to the anatomical evidence favoring such an interpretation, Hatschek ('80, pp. 60–62) has recently advanced strong evidence from an embryological standpoint for believing that they are nephridia which primitively opened directly to the exterior.

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[1] By this suggestion, Semper allows some justification to W. Müller's conception of a pronephros, although he had earlier contested it.

Among the attempts to find a homologue of the segmental duct already present in the Worms may be mentioned the longitudinal canal described by Hatschek ('78, p. 117 *seq.*) in the larva of Polygordius. Were Hatschek's account accurate, it would doubtless warrant great changes in our conceptions of the interrelationships of the Vermian nephridia, and of the origin of the Vertebrate kidneys; but his statements have not been confirmed by any subsequent observations, though several investigators have concerned themselves with this interesting form (Fraipont, '87, p. 83; Eisig, '87, p. 662; E. Meyer, '87, p. 594; Bergh, '85, p. 27, footnote).

The remaining views in respect to the nature of the duct agree in regarding it as a secondary growth.[1] Beard ('87, p. 651) and Haddon ('87) accept the ectodermal origin of the segmental duct, and endeavor to give it phylogenetic significance by assuming that the ontogenetic connection of the duct with the ectoderm indicates that it was represented in the phylogeny at first by a groove into which the nephridia opened, and that this groove gradually became closed and was cut off as a tube extending from the most anterior tubule backwards to the cloaca. Rückert ('88) and van Wijhe ('89, pp. 507, 508), on the other hand, assert a gradual backward growth of a primitively anterior opening.

None of these views are compatible with the fact that in many Vertebrates the duct is demonstrably of mesodermal origin. They also seem to me to give insufficient significance to the mode in which the pronephric diverticula unite to form a longitudinal canal; and the first two authors neglect it wholly.

Finally, the abandoned view of Balfour ('76, pp. 25, 26), according to which *the duct arises by the fusion of the distal ends of the several nephridia*, has been revived by Eisig ('87, p. 649), and was accepted by Rückert ('88, p. 264) for the *pronephric portion* of the duct. This view seems to me much the most probable, and I am inclined to accept it.

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[1] Here belongs also the view of Boveri ('90), which has already been discussed (page 265).

In the foregoing discussion, I have endeavored to show that there is considerable evidence in favor of the view that the excretory system of Vertebrates has developed from a system of metameric nephridia, such as are present in Annelids. None of the evidence seems to me, however, final. The excretory systems of the two groups are very similar, but we have no means of limiting definitely the part that has been played by physiologically similar needs in moulding the structure of the organs. Nor am I committed to the theory of the Annelidan extraction of Vertebrates. I fully realize that such a theory can only be established by investigations which shall include in their scope the entire organization of the two groups. So far as this larger theory has been dealt with in this discussion, it has been with the view of contributing such evidence as the excretory system offers, and I have naturally left untouched the mass of evidence which proceeds from other organs. To this in addition we must appeal for the justification of the broader theory.

Cambridge, April 25, 1891.

BIBLIOGRAPHY.

Ackeren, F. van.

'89. Beiträge zur Entwickelungsgeschichte der weiblichen Sexualorgane des Menschen. Zeitschr. f. wiss. Zool., Bd. XLVIII. pp. 1–46, Taf. I.–III. 5 Apr., 1889.

Artemjeff, A. P.

'89. О микроскопическомъ изслѣдованій послѣродовыхъ отдѣленій. Врачъ, Т. X. № № 35 и 36, 1889 года, Стр. 769–770 и 791–795, 8 Рис. 31–го августа и 7–го септября.

[On Microscopical Examinations of Puerperal Discharges. The Physician, Vol. X. Nos. 35, 36, pp. 769–770 and 791–795, 8 woodcuts. 31 Aug. and 7 Sept., 1889.]

Ayers, Howard.

'85. Beiträge zur Anatomie und Physiologie der Dipnoër. Jena. Zeitschr. f. Naturwiss., Bd. XVIII. pp. 479–527, Taf. XVI.–XVIII. 1885.

'90. Contribution to the Morphology of the Vertebrate Head. Zool. Anzeig., Bd. XIII. pp. 504–507. 15 Sept., 1890.

Balfour, Francis M.

'75. On the Origin and History of the Urinogenital Organs of Vertebrates. Jour. of Anat. and Physiol., Vol. X. pp. 17–48. Oct., 1875.

'78. A Monograph on the Development of Elasmobranch Fishes. xi + 295 pp., 20 Pls., 9 woodcuts. London: Macmillan & Co. 1878.

'81^{a}. A Treatise on Comparative Embryology. Vol. II., xi + 655 + xxii pp., 429 Figs. London: Macmillan & Co. 1881.

'81^{b}. Die "Kopfniere" der ausgewachsenen Teleostier und Ganoiden. Biol. Centralbl., Bd. I. pp. 459–461. 15 Nov., 1881.

'82. On the Nature of the Organ in Adult Teleosteans and Ganoids, which is usually regarded as the Head-Kidney or Pronephros. Quart. Jour. Micr. Sci., Vol. XXII. pp. 12–16. Jan., 1882.

Balfour, F. M., and W. N. Parker.

'82. On the Structure and Development of Lepidosteus. Philos. Trans. Roy. Soc. London, Vol. CLXXIII. Pt. II. pp. 359–442, Pl. XXI.–XXIX., 4 woodcuts. 1882.

Balfour, F. M., and Adam Sedgwick.

'78. On the Existence of a Rudimentary Head-Kidney in the Embryo Chick. Proc. Roy. Soc. London, Vol. XXVII. No. 188, pp. 443–446. 1878.

'79. On the Existence of a Head-Kidney in the Embryo Chick, and on Certain Points in the Development of the Müllerian Duct. Quart. Jour. Micr. Sci., Vol. XIX. pp. 1–20, Pl. I., II. Jan., 1879.

Bambeke, Ch. van.

'80. Nouvelles récherches sur l'embryologie des Batraciens. Arch. de Biol., Tom. I. pp. 305–380, Pl. XI.–XIV. 1880.

Beard, John.

'87. The Origin of the Segmental Duct in Elasmobranchs. Anat. Anzeig., Bd. II. pp. 646–652. 1 Okt., 1887.

'88. Morphological Studies. II. The Development of the Peripheral Nervous System of Vertebrates. Pt. 1, Elasmobranchii and Aves. Quart. Jour. Micr. Sci., Vol. XXIX. pp. 153–227, Pl. XVI.–XXI. Oct., 1888.

'89. On the Early Development of *Lepidosteus osseus* (Prelim. Notice). Proc. Roy. Soc. London, Vol. XLVI., pp. 108–118. 16 May, 1889.

'90. The Inter-relationships of the Ichthyopsida. A Contribution to the Morphology of Vertebrates. Anat. Anzeig., Bd. V. pp. 146–159, 179–188. März, 1890.

Bergh, R. S.

'85. Die Excretionsorgane der Würmer. Eine Uebersicht. Kosmos, Bd. XVII. pp. 97–122, Taf. II. 1885.

'88. Zur Bildungsgeschichte der Excretionsorgane bei Criodrilus. Arb. zool.-zoot. Inst. Würzburg, Bd. VIII. pp. 223–248, Taf. XIII., XIV. 1888.

'90. Neue Beitrage zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzirung des Keimstreifens von Lumbricus. Zeitschr. f. wiss. Zool., Bd. L. pp. 469–526, Taf. XIX.–XXI. 2 Sept., 1890.

Bidder, F. H.

'46. Vergleichend-anatomische und histologische Untersuchungen über die männlichen Geschlechts- und Harnwerkzeuge der nackten Amphibien. 74 pp., 3 Taf. Dorpat. 1846.

Birch-Hirschfeld, F. V.

'89. Lehrbuch der allgemeinen pathologischen Anatomie. 4te Auflage. xxii + 486 pp., 176 Abbild. im Text. Leipzig: Vogel. 1889.

Böhmig, L.

'90. Untersuchungen über rhabdocöle Turbellarien. II. Plagiostomum und Cylindrostomum Graff. Zeitschr. f. wiss. Zool., Bd. LI. pp. 167–479, Taf. XII.–XXI. 31 Dez., 1890.

[*Also in* Arb. zool. Inst. Graz, Bd. IV. No. 1.]

Bonnet, R.

'87. Ueber die ectodermale Entstehung des Wolff'schen Ganges bis den Säugethieren. Sitz.-Ber. Gesellsch. Morph. u. Physiol. München, Bd. III. pp. 104–112. 1887.

'88. Präparate und Zeichnungen zur Entwickelungsgeschichte des Schafes. (Demonstr. in der 3ten Sitz. der Anatomischen Gesellschaft auf der 2ten Versamml. in Würzburg.) Anat. Anzeig., Bd. III. pp. 714–717. 15 Aug., 1888.

Bornhaupt, Theodor.

'67. Untersuchungen über die Entwickelung des Urogenitalsystems beim Hühnchen. Inaug. Diss. Dorpat. 48 pp., 3 Taf. Riga. 1867.

Boveri, Th.

'90. Ueber die Niere des Amphioxus. (Vortr. geh. in der Gesellsch. f. Morph. u. Physiol. in München am 3. Juni, 1890.) München. med. Wochenschr., Bd. XXXVII. No. 26, pp. 452–455, 2 Holzschn. 1 Juli, 1890.

[*Also in* Sitz.-Ber. Gesellsch. f. Morph. u. Physiol. München, Bd. VI. Heft 2, pp. 65–77.]

Braun, Max.

'77. Urogenitalsystem der einheimischen Reptilien entwicklungsgeschichtlich und anatomisch bearbeitet. Arb. zool.-zoot. Inst. Würzburg, Bd. IV. pp. 113–228, Taf. V.–X. 1877.

'79. Aus der Entwickelungsgeschichte der Papageien. Tagebl. d. 52. Vers. deutsch. Naturf. u. Aerzte in Baden-Baden. Ber. ü. d. Sitz. d. Sect. f. Zool. u. vergl. Anat., pp. 227–229, 2te Sitz. v. 22 Sept., 1879.

Brook, George.

'87. Note on the Epiblastic Origin of the Segmental Duct in Teleosts and Birds. Proc. Roy. Soc. Edinburgh, Vol. XIV. pp. 368–370. 1887.

Bürger, Otto.

'90. Untersuchungen über die Anatomie und Histologie der Nemertinen nebst Beiträgen zur Systematik. Zeitschr. f. wiss. Zool., Bd. L. pp. 1–277, Taf. I.–X., 10 Fig. in Text. 10 Juni, 1890.

Calderwood, W. L.

'91. The Head-Kidney of Teleostean Fishes. Jour. Mar. Biol. Ass., Vol. II. No. 1, pp. 43–46, Pl. I. May, 1891.

Carius, Friedrich.

'88. Ueber die Entwickelung der Chorda und der primitiven Rachenhaut bei Meerschweinchen und Kaninchen. Inaug. Diss. Marburg, 33 pp., 1 Taf. 1888.

Chun, Carl.

'80. Die Ctenophoren des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna u. Flora d. G. v. Neapel, Monogr. I., xviii + 313 pp., 16 Taf. in Lith., 22 Holzschn. Leipzig: Engelmann. 1880.

Claparède, Edouard.

'69. Histologische Untersuchungen über den Regenwurm (Lumbricus terrestris Linné). Zeitschr. f. wiss. Zool., Bd. XIX. pp. 563–624, Taf. XLIII.–XLVIII. 6 Nov., 1869.

Clarke, Samuel F.

'81. The Early Development of the Wolffian Body in Amblystoma punctatum. Stud. Biol. Lab. Johns Hopkins Univ., Vol. II. pp. 39–44, Pl. I.–III. June, 1881.

Cunningham, J. T.

'87ª. The Nephridia of Lanice conchilega Malmgren (Prelim. Notice). Nature, Vol. XXXVI. pp. 162, 163. 16 June, 1887.

'87ᵇ. On some Points in the Anatomy of Polychæta. Quart. Jour. Micr. Sci., Vol. XXVIII. pp. 239–278, Pl. XVII.–XIX. Nov., 1887.

Dansky, J., und J. Kostenitsch.

'80. Ueber die Entwickelungsgeschichte der Keimblätter und des Wolff'schen Ganges im Hühnerei. Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 7, Tom. XXVII. No. 13, 25 pp., 2 Taf. Sept., 1880.

Dursy, Emil.

'67. Der Primitifstreif des Hühnchens. 80 pp., 38 Abbild. auf 3 Taf. Lahr: Schaumburg & Cie. 1867.

Duval, Matthias.

'82. Sur le développement de l'appareil génito-urinaire de la Grenouille. I. Le rein précurseur. 32 pp., 2 Pl. Montpellier: Böhm et Fils. 1882. [*Also in* Rev. des Sci. Nat., Sér. 3, Tom. I.]

Ecker, Alexander.

'64–'82. Die Anatomie des Frosches. I. Knochen- und Muskellehre. vi + 139 pp., 96 Fig. Braunschweig, 1864. II. Nerven und Gefässlehre. Mit Beiträgen von R. Wiedersheim. vi + 115 pp., 1 Taf., 64 Fig. Braunschweig, 1881. III. Lehre von den Eingeweiden, dem Integument und den Sinnesorganen. Bearbeitet von R. Wiedersheim. vi + 95 pp., 1 Taf., 35 Fig. Braunschweig, 1882.

Eisig, Hugo.

'78. Die Segmentalorgane der Capitelliden. (Auszug) Mitth. zool. Stat. Neapel, Bd. I. pp. 93–118, Taf. IV. 1878.

'87. Monographie der Capitelliden des Golfes von Neapel und den angrenzenden Meeres-Abschnitten nebst Untersuchungen zur vergleichenden Anatomie und Physiologie. Fauna u. Flora d. G. v. Neapel, Monogr. XVI., xxvi + 906 pp., 20 Holzschn., 37 Taf. in Lith. Berlin: Friedländer. 1887.

Emery, Carlo.

'80. Le specie del genre Fierasfer nel Golfo di Napoli e regioni limitrofe. Fauna u. Flora d. G. v. Neapel, Monogr. II., 76 pp., 9 Tav. lit., 10 incis. in legno. Leipzig: Engelmann. 1880.

'81. Morphologie der Kopfniere der Teleostier. Biolog. Centralbl., Bd. I. pp. 527–529. 15 Dec., 1881.

'82. Studi intorno allo sviluppo ed alla morfologia del rene dei Teleostei. Mem. Reale Accad. dei Lincei, Cl. Sc. fis. ecc., Ser 3a, Vol. XIII. pp. 43–50, 1 Tav. 1882.

[*Abstract given in* Arch. ital. de Biol., Tom. II. pp. 135–145.]

'85. Zur Morphologie der Kopfniere der Teleostier; Erwiderung an Herrn S. Grosglik. Zool. Anzeig., Bd. VIII. pp. 742–744. 28 Dec., 1885.

Felix, Walther.

'90. Zur Entwickelungsgeschichte der Vorniere des Hühnchens. Anat. Anzeig., Bd. V. pp. 526–530. 12 Sept., 1890.

Fleischmann, A.

'87. Zur Entwickelungsgeschichte der Raubthiere. Biol. Centralbl., Bd. VII. pp. 9–12. 1 März, 1887.

Flemming, Walther.

'86. Die ektoblastiche Anlage des Urogenitalsystems beim Kaninchen. Arch. f. Anat. u. Physiol., Jahrg. 1886, Anat. Abt., pp. 236–248, Taf. XI. 18 Aug., 1886.

Foster, M., and F. M. Balfour.

'74. The Elements of Embryology. xix + 272 pp., 71 Figs. London: Macmillan. 1874.

'83. The Elements of Embryology. 2d Edit. Revised. Edited by Adam Sedgwick and Walter Heape. xiv + 486 pp., 141 Figs. London: Macmillan. 1883.

Fraipont, Julien.

'80^a. Recherches sur l'appareil excréteur des Trématodes et des Cestodes. Arch. de Biol., Tom. I. pp. 415–456, Pl. XVIII., XIX., 1 Fig. 20 Août, 1880.

'80^b. Recherches sur l'appareil excréteur des Trématodes et des Cestodes. (Deuxième Partie.) Arch. de Biol., Tom. II. pp. 1–40, Pls. I., II. 1881.

'87. Le genre Polygordius. Fauna u. Flora d. G. v. Neapel, Monogr. XIV., xiv + 125 pp., 16 Pl. lith., 1 Fig. dans le Texte. Berlin: Friedländer. 1887.

Francotte, P.

'81. Sur l'appareil excréteur des Turbellariés rhabdocœles et dendrocœles (Comm. Prélim.). Bull. Acad. Roy. Belgique, Ann. 50, Sér. 3, Tom. I. pp. 30–34, 1 Pl. 1881.

'83. Note sur l'anatomie et l'histologie d'un Turbellarié rhabdocèle. Bull. Acad. Roy. Belgique, Ann. 52, Sér. 3, Tom. VI., pp. 723–735, 1 Pl. 1883.

Furbringer, Max.

'77. Zur Entwickelung der Amphibienniere. (Inaug. Diss.) viii + 124 pp., 3 Taf. Heidelberg: Hörning. 1877.

'78^a. Zur vergleichenden Anatomie und Entwickelungsgeschichte der Excretionsorgane der Vertebraten. Morph. Jahrb., Bd. IV. pp. 1–111, Taf. I.–III. 1878.

'78^b. Ueber die Homologie der sog. Segmentalorgane der Anneliden und Wirbelthiere. Morph. Jahrb., Bd. IV., pp. 663–678. 1878.

'79. Ueber den principiellen Standpunct des Herrn Prof. Semper. Morph. Jahrb., Bd. V. pp. 396, 397. 1879.

Gadow, Hans.

'88. Remarks on the Cloaca and the Copulatory Organs of the Amniota. Phil. Trans. Roy. Soc. London, Vol. CLXXVIII. B., pp. 5–37, Pl. II.–V. 1888.

Gasser, E.

'74. Beiträge zur Entwicklungs-Geschichte der Allantois der Müller'schen Gänge und des Afters. (Acad. Habilitationsschr. Marburg.) 75 pp., 3 Taf. Frankfurt: Winter. 1874.

'75. Die Entstehung des Wolff'schen Ganges beim Huhn. Sitz.-Ber. d. naturf. Gesellsch. Marburg, Jahrg. 1875, Nro. 1 u. 2, pp. 21–23. Jan., Feb., 1875.

'77. Beobachtungen über die Entstehung des Wolff'schen Ganges bei Embryonen von Hühnern und Gänsen. Arch. f. mikr. Anat., Bd. XIV. pp. 442–459, nebst 2 als Anhang ausgegeb. Taf. 1877.

'82. Zur Entwicklung von Alytes obstetricans. Sitz.-Ber. d. naturf. Gesellsch. Marburg, Jahrg. 1882, Nro. 5, pp. 73–97. Oct., 1882.

Gasser, E., und Siemerling.

'78. Das obere Ende des Wolff'schen Ganges im Hühnerei. Sitz.-Ber. d. naturf. Gesellsch. Marburg, Jahrg. 1878, Nro. 3, pp. 62–65. Nov., 1878.

'79. Beiträge zur Entwickelung des Urogenitalsystems der Huhnerembryonen. Sitz.-Ber. d. naturf. Gesellsch. Marburg, Jahrg. 1879, Nro. 5, pp. 58–65. Juni, 1879.

Gegenbaur, Carl.

'78. Grundriss der vergleichenden Anatomie. 2te verb. Aufl., viii + 655 pp., 356 Fig. in Holzschn. Leipzig: Engelmann. 1878.

Giacosa, Piero.

'82. Études sur la composition chimique de l'œuf et de ses enveloppes chez la Grenouille commune. I. Sur l'enveloppe muqueuse de l'œuf. Zeitschr. f. physiol. Chemie, Bd. VII. pp. 40–56. Nov., 1882.

[*Abstract given in* Arch. Ital. Biol., Tom. II. pp. 226–230.]

Giles, Arthur E.

'88. Development of the Fat-bodies in Rana temporaria. A Contribution to the History of the Pronephros. Quart. Jour. Micr. Sci., Vol. XXIX. pp. 133–142, Pl. XIV. Oct., 1888.

Goette, Alexander.

'75. Entwickelungsgeschichte der Unke (Bombinator igneus). viii + 964 pp., m. Atlas v. 22 lith. Taf. Leipzig: Voss. 1875.

'88. Ueber die Entwickelung von Petromyzon fluviatilis (vorl. Mitth.). Zool. Anzeig., Bd. XI. pp. 160–163. 26 März, 1888.

Graff, Ludwig von.

'82^a. Monographie der Turbellarien. I. Rhabdocœlida. xii + 441 pp., 12 Holzschn., Atlas mit 20 Taf. Leipzig: Engelmann. 1882.

'82^b. Ueber Rhodope Veranii Kölliker. Morph. Jahrb., Bd. VIII. pp. 73–84, Taf. II. 1882.

Grobben, Carl.

'88. Die Pericardialdrüse der chaetopoden Anneliden, nebst Bemerkungen über die perienterische Flüssigkeit derselben. Sitz.-Ber. d. k. Akad. Wiss. Wien, matth.-naturh. Cl., Bd. XCVII. Abt. 1, pp. 250–263. 1888.

Grosglik, S.

'85. Zur Morphologie der Kopfniere der Fische. Zool. Anzeig., Bd. VIII. pp. 605–611. 12 Oct., 1885.

'86. Zur Frage über die Persistenz der Kopfniere der Teleostier. Zool. Anzeig., Bd. IX. pp. 196–198. 29 März, 1886.

Gruby.

'42. Recherches anatomiques sur le système veineux de la Grenouille. Ann. Sci. Nat., Sér. 2, Tom. XVII., Zool., pp. 209–230, Pl. IX., X. 1842.

Günther, Albert.

'58. Catalogue of the Batrachia Salientia in the Collection of the British Museum. xvi + 160 pp., 12 Pl. London. 1858.

Haddon, Alfred C.

'87. Suggestion respecting the Epiblastic Origin of the Segmental Duct. Sci. Proc. Roy. Soc. Dublin, Vol. V., N. S., Pt. 6, pp. 463–472, Pl. X. April, 1887.

Haeckel, Ernst.

'74^a Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblätter. Jena. Zeitschr. f. Naturwiss., Bd. VIII. pp. 1–55, Taf. I., 4 phylogen. Tabellen. 1874.

'74^b. Anthropogenie oder Entwickelungsgeschichte des Menschen. xviii + 732 pp., 12 Taf., 210 Holzschn., 36 genet. Tab. Leipzig: Engelmann. 1874.

Hatschek, Berthold.

'78. Studien über Entwicklungsgeschichte der Anneliden. Arb. zool. Inst. Wien, Bd. I. Heft 3, pp. 277–404, Taf. XXIII.–XXX. 1878.

'80. Ueber Entwicklungsgeschichte von Echiurus und die systematische Stellung der Echiuriden (Gephyrei chætiferi). Arb. zool. Inst. Wien, Bd. III. pp. 45–78, Taf. IV.–VI. 1880.

'84. Mittheilungen über Amphioxus. Zool. Anzeig., Bd. VII. pp. 517–520. 29 Sept., 1884.

'88^a. Lehrbuch der Zoologie. 1te Lieferung, iv + 144 pp., 155 Abbild. im Text. Jena: Fischer, 1888.

'88^b. Ueber den Schichtenbau von Amphioxus. Vortrag in der 3ten Sitz. d. Anat. Gesellsch. auf der 2ten Versamml. in Würzburg. Anat. Anzeig., Bd. III. pp. 662–667, 5 Abbild. [Diskussion, pp. 673–679.] 15 Aug., 1888.

Henneguy, Félix.

'88, '89. Recherches sur le développement des Poissons osseux. Embryogénie de la Truite. Journ. de l'Anat. et Physiol., Année XXIV., pp.

413–502, 24 Fig.; pp. 525–617, Pl. XVIII.–XXI. 16 Dec., 1888, and 20 Feb., 1889.

Hensen, Victor.

'66. Bemerkungen über die Lymphe. Arch. f. pathol. Anat., Bd. XXXVII. pp. 68–93. Sept., 1866.

'67. Embryologische Mittheilungen. Arch. f. mikr. Anat., Bd. III. pp. 500–503. 1867.

'75, '76. Beobachtungen über die Befruchtung und Entwickelung des Meerschweinchens und Kaninchens. Arch. f. Anat. u. Physiol., Jahrg. 1875, Anat. Abt. (His u. Braune's Zeitschr., Bd. I.), pp. 213–273, 353–423, Taf. VIII.–XII. 26 Nov., 1875, 20 März, 1876.

Hertwig, Oscar.

'83. Die Entwicklung des mittleren Keimblattes der Wirbelthiere. vi + 128 pp., 9 Taf. Jena: Fischer. 1883.

'88. Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbelthiere. 2te verm. u. verb. Aufl., xii + 519 pp., 304 Abbild. im Text, 2 lith. Taf. Jena: Fischer. 1888.

His, Wilhelm.

'65^a. Die Häute und Höhlen des Körpers. Acad. Progr. Basel, 34 pp. 1865.

'65^b. Beobachtungen über den Bau des Säugethiereierstockes. Arch. f. mikr. Anat., Bd. I. pp. 151–202, Taf. VIII.–XI. 1865.

'68. Untersuchungen über die erste Anlage des Wirbelthierleibes. Die erste Entwicklung des Hühnchensim Ei. xvi + 237 pp., 12 Taf. Leipzig. 1858.

Hoffmann, C. K.

'86. Zur Entwickelungsgeschichte der Urogenitalorgane bei den Anamnien. Zeitschr. f. wiss. Zool., Bd. XLIV. pp. 570–643, Taf. XXXIII.–XXXV., 4 Holzschn. 14 Dec., 1886.

'89. Zur Entwickelungsgeschichte der Urogenitalorgane bei den Reptilien. Zeitschr. f. wiss. Zool., Bd. XLVIII., pp. 260–300, Taf. XVII., XVIII., 1 Holzschn. 28 Juni, 1889.

Houssay, Frédéric.

'91. Etudes d'embryologie sur les Vertebrés. IV. Les Fentes Branchiales. Bull. sci. de la France et de la Belgique, Tom. XXIII. pp. 55–79, Pl. I–III. 21 Févr., 1891.

Hoyer, Heinrich.

'90. Ueber den Nachweis des Mucins in Geweben mittelst der Färbemethode. Arch. f. mikr. Anat., Bd. XXXVI. pp. 310–374. 27 Sept., 1890.

Huxley, Thomas H.

'76. On the Classification of the Animal Kingdom. Jour. Linn. Soc., Vol. XII., Zoöl., pp. 199–226. (Read Dec. 3, 1874.) 1876.

Hyrtl, J.

'51. Das uropoetische System der Knochenfische. Denkschr. d. k. Akad. Wiss. Wien, math.-naturwiss. Cl. Bd. II. pp. 27–100, Tab. IX.–XVII. 1851.

Iijima, Isao.

'84. Untersuchungen über den Bau und die Entwicklungsgeschichte der Susswasser-Dendrocoelen (Tricladen). Zeitschr. f. wiss. Zool., Bd. XL. pp. 359–464, Taf. XX.–XXIII. 27 Juni, 1884.

Janošik, J.

'85. Histologisch-embryologische Untersuchungen über das Urogenitalsystem. Sitz.-Ber. d. k. Akad. Wiss. Wien, Bd. XCI., math.-naturwiss. Cl., Abt. 3, Febr.-Heft, pp 97–199, 4 Taf. 1885.

'87. Zwei junge menschliche Embryonen. Arch. f. mikr. Anat., Bd. XXX. pp. 559–595, Taf. XXXIV., XXXV. 18 Nov., 1887.

Kastschenko, N.

'87. Das Schlundspaltengebiet des Hühnchens. Arch. f. Anat. u. Physiol., Jahrg. 1887, Anat. Abt., pp. 258–300, Taf. XVII.–XIX. 8 Dec., 1887.

Keibel, Franz.

'88a. Zur Entwicklungsgeschichte des Igels (Erinaceus europæus). Anat. Anzeig., Bd. III. pp. 631–637, 1 Abbild. 1 Aug., 1888.

'88b. Die Entwickelungsvorgänge am hinteren Ende des Meerschweinchenembryos. Arch. f. Anat. u. Phisiol., Jahrg. 1888, Anat. Abt., pp. 407–430, Taf. XXIII., XXIV. 5 Oct., 1888.

Kellogg, J. L.

'90. Notes on the Pronephros of Amblystoma punctatum. Johns Hopkins Univ. Circ., Vol. IX. No. 80, p. 59. April, 1890.

Klebs, Edwin.

'89. Die allgemeine Pathologie oder die Lehre von den Ursachen und dem Wesen der Krankheitsprocesse. 2te Th. Störungen des Baues und der Zusammensetzung. xx + 837 pp., 79 farb. Abbild. im Text, 47 Farbentaf. Jena: Fischer. 1889.

Kölliker, Albert von.

'61. Entwickelungsgeschichte des Menschen und der höheren Thiere. x + 468 pp., 225 Holzschn. Leipzig: Engelmann. 1861.

'79. Entwickelungsgeschichte des Menschen und der höheren Thiere, 2te Aufl. xxxiv + 1033, 606 Fig. im Text. Leipzig: Engelmann. 1879.

Köllmann, Jul.

'82a. Die Doppelnatur des excretorischen Apparates bei den Cranioten. Zool. Anzeig., Bd. V. pp. 522–524. 9 Oct., 1882.

'82b. Ueber Verbindungen zwischen Coelom und Nephridium. Festschr. z. Feier d. 300 jährigen Best. d. Univ. Würzburg gew. v. d. Univ. Basel, pp. 1–59, Taf. I., II. 1882.

'91. Die Rumpfsegmente menschlicher Embryonen von 13 bis 35 Urwirbeln. Arch. f. Anat. u. Physiol., Jahrg. 1891, Anat. Abt., Heft 1, pp. 66–88, Taf. III.–V. 19 Mai, 1891.

Kowalewsky, A.

'67. Entwickelungsgeschichte des Amphioxus lanceolatus. Mém. Acad. Imp. Sci. St.-Pétersbourg, Sér. 7, Tom. XI. No. 4, 17 pp., 3 Taf. 1867.

Kowalewsky, A., Ph. Owsjannikow und N. Wagner.

'70. Die Entwickelungsgeschichte der Störe. Vorläufige Mittheilung. Bull. Acad. Imp. Sci. St.-Pétersbourg, Tom. XIV. pp. 317–325, 7 Fig. 1870.

Kowalewsky, R.

'75. Образованіе началъ мочелополовыхъ органовъ у куриныхъ зародышей. Труды Лаборат. Варшав. Унив. Вып. II., стр. 149–208. 1875.

[The Origin of the Fundaments of the Urogenital Organs in Chick Embryos. Stud. Lab. Warsaw Univ., No. II. pp. 149–208. 1875.]

Kükenthal, Willy.

'85. Ueber die lymphoiden Zellen der Anneliden. Jena. Zeitschr. f. Naturwiss., Bd. XVIII. pp. 319–364, Taf. X., XI. 10 Feb., 1885.

Kupffer, Carl.

'88. Ueber die Entwicklung von Petromyzon Planeri. Sitz.-Ber. d. k. b. Akad. Wiss. München, math.-phys. Cl., Heft 1, Sitz. v. 4 Feb., 1888. pp. 71–79. 1888.

Lang, Arnold.

'81. Der Bau von Gunda segmentata und die Verwandtschaft der Platyhelminthen mit Coelenteraten und Hirudineen. Mitth. Zool. Stat. Neapel, Bd. III. pp. 187–251, Taf. XII.–XIV. 9 Dec., 1881.

'84. Die Polycladen (Seeplanarien) des Golfes von Neapel und der angrenzenden Meeres-Abschnitte. Fauna u. Flora d. G. v. Neapel, Monogr. XI., ix + 688 pp., 54 Holzschn., 39 lith. Taf. Leipzig: Engelmann. 1884.

Langerhaus, Paul.

'76. Zur Anatomie des Amphioxus lanceolatus. Arch. f. mikr. Anat., Bd. XII. pp. 290–348, Taf. XII.–XV. 1876.

Lankester, E. Ray.

'75. On some New Points in the Structure of Amphioxus and their Bearing on the Morphology of Vertebrata. Quart. Jour. Micr. Sci., Vol. XV. pp. 257–267, 4 woodcuts. July, 1875.

'89. Contributions to the Knowledge of Amphioxus lanceolatus Yarrell. Quart. Jour. Micr. Sci., Vol. XXIX. pp. 365–408, Pl. XXXIV.–XXXVI., XXXVI^{a}., XXXVI^{b}. April, 1889.

Lankester, E. Ray, and Arthur Willey.

'90. The Development of the Atrial Chamber of Amphioxus. Quart. Jour. Micr. Sci., Vol. XXXI. pp. 445–466, Pl. XXIX.–XXXII., 9 woodcuts. August, 1890.

Lockwood, C. B.

'87. The Development and Transition of the Testis, Normal and Abnormal. Jour. Anat. and Physiol., Vol. XXI. pp. 635–664, Pl. XV. July, 1887.

McIntosh, Wm. Carmichael, and E. E. Prince.

'88. On the Development and Life-Histories of the Teleostean Food- and other Fishes. Trans. Roy. Soc. Edinburgh, Vol. XXXV. pp. 665–946, Pl. I.–XXVIII. 1888.

Marcussen, Jean.

'51. Sur le développement des parties génitales et uropoiëtiques chez les Batraciens. Gazette Méd. de Paris, 1851.

[*Quoted from* Duval, '82.]

Marshall, A. Milnes, and Edward J. Bles.

'90^a. The Development of the Kidneys and Fat-Bodies in the Frog. Stud. Biol. Lab. Owens College., Vol. II. pp. 133–158, Pl. X. 1890.

'90^b. The Development of the Blood-vessels in the Frog. Stud. Biol. Lab. Owens College, Vol. II. pp. 185–268, Pl. XIII.–XV. 1890.

Martin, E.

'88. Ueber die Anlage der Urniere beim Kaninchen. Inaug. Diss. Marburg. Arch. f. Anat. u. Physiol., Jahrg. 1888, Anat. Abt., pp. 109–123, Taf. VII. 15 Juni, 1888.

Mayer, Paul.

'87. Ueber die Entwickelung des Herzens und der grossen Gefässstämme bei den Selachiern. Mitth. zool. Stat. Neapel, Bd. VII. pp. 338–370, Taf. XI., XII. 18 April, 1887.

Meyer, Eduard.

'82. Zur Anatomie und Histologie von Polyophthalmus pictus Clap. Arch. f. mikr. Anat., Bd. XXI. pp. 769–823, Taf. XXXII., XXXIII. 28 Oct., 1882.

'87. Studien über den Körperbau der Anneliden. Mitth. zool. Stat. Neapel, Bd. VII. pp. 592–741, Taf. XXII.–XXVII. 22 Dec., 1888.

Meyer, Hans.

'90. Die Entwickelung der Urniere beim Menschen. Arch. f. mikr. Anat., Bd. XXXVI. pp. 138–172, Taf. V.–VI. 1890.

Mihalkovics, Geza von.

'84. Untersuchungen über die Entwickelung der Harn- und Geschlechtsorgane der Vertebraten. I. Die Primordialnieren (Nephridien) der Amnioten. Math. u. naturwiss. Ber. aus Ungarn, Bd. II. pp. 178–183. 1884.

[Translated from Math. és. Természettud. Értesito″, Bd. II.]

'85. Untersuchungen über die Entwickelung des Harn- und Geschlechtsapparates der Amnioten. (Auszug) Internat. Monatschr. f. Anat. u. Physiol., Bd. II. pp. 41–62, 65–106, 284–339, 348–385, 387–433, 435–485, Taf. I.–IX., IX. A. 1885.

[Abstract of A gerinczes állatok kiválaszto' és ivarszerveinek fejlödése. 380 pp., 10 Tab.]

Mitsukuri, K.

'88. The Ectoblastic Origin of the Wolffian Duct in Chelonia. (Prelim. Notice.) Zool. Anzeig., Bd. XI. p. 111. 5 März, 1888.

Mollier, S.

'90. Ueber die Entstehung des Vornierensystems bei Amphibien. Arch. f. Anat. u. Physiol., Jahrg. 1890, Anat. Abt., pp. 207–235, Taf. XI., XII., 1 Holzschn. 20 Juni, 1890.

Müller, Johannes.

'29. Ueber die Wolff'schen Korper bei den Embryonen der Frösche und Kröten. Meckel's Arch. f. Anat. u. Physiol., Jahrg. 1829, pp. 65–70, Taf. III. 1829.

'30. Bildungsgeschichte der Genitalien. xviii + 152 pp., 4 Taf. Düsseldorf. 1830.

'44. Ueber den Bau und die Lebenserscheinungen des Branchiostoma lubricum Costa, Amphioxus lanceolatus Yarrell. Abhandl. d. k. Acad. Wiss. Berlin, 1842, pp. 79–116, Taf. I.–V. 1844.

Müller, Wilhelm.

'75. Das Urogenitalsystem des Amphioxus und der Cyclostomen. Jena. Zeitschr. f. Naturwiss., Bd. IX. pp. 94–129, Taf. IV., V. 1875.

Nagel, W.

'89. Ueber die Entwickelung des Urogenitalsystems des Menschen. Arch. f. mikr. Anat., Bd. XXXIV. pp. 269–384, Pl. XVII.–XX. 2 Dec., 1889.

Oellacher, J.

'73. Beiträge zur Entwicklungsgeschichte der Knochenfische nach Beobachtungen am Bachforelleneie III.–V. Zeitschr. f. wiss. Zool., Bd. XXIII. pp. 1–115, Taf. I.–IV. 30. Jan., 1873.

Orr, Henry.

'87. Contribution to the Embryology of the Lizard. Jour. of Morph., Vol. I. pp. 311–372, Pl. XII.–XVI. Dec., 1887.

Ostroumoff, A.

'88^{a}. Zur Entwicklungsgeschichte der Eidechsen. Zool. Anzeig., Bd. XI. pp. 620–622. 5 Nov., 1888.

'88^{b}. Къ исторіи развитія ящерицъ. Труды Общества Естествоиспытателей при ИМП. Казан. Унив. Т. XIX. вып. 122 стр., 3 Таб. Казань, 1888.

[Contributions to the Developmental History of the Lizard. Mem. Soc. Naturalists Univ. Kasan, Vol. XIX. Part 3, 122 pp., 3 Pl. Kasan, 1888.]

Oudemans, A. C.

'85. The Circulatory and Nephridial Apparatus of the Nemertea. Quart. Jour. Micr. Sci., Vol. XXV., Suppl., pp. 1–80, Pl. I.–III. 1885.

Overlach, M.

'85. Die pseudo-menstruirende Mucosa uteri nach acuter Phosphorvergiftung. Arch. f. mikr. Anat., Bd. XXV. pp. 191–235, Taf. X., XI. 18 Juli, 1885.

Owen, Richard.

'66. On the Anatomy of Vertebrates. Vol. I. Fishes and Reptiles. xlii + 650 pp., 452 Fig. London: Longmans, Green, & Co. 1866.

Owsjanniskow, Ph.

'89. Zur Entwickelungsgeschichte des Flussneunaugens (Vorl. Mitth.). Bull. Acad. Imp. Sci. St.-Pétersbourg, Tom. XXXIII. No. 1, pp. 83–95. Avril, 1889.

Parker, W. Newton.

'88. Zur Anatomie und Physiologie von Protopterus annectans. Ber. naturf. Gesellsch. Freiburg, Bd. IV. pp. 83–108. 1888.

Perenyi, Josef von.

'87. Die ektoblastische Anlage des Urogenitalsystems bei Rana esculenta und Lacerta viridis. Zool. Anzeig., Bd. X. p. 66. 31 Jan., 1887.

'88. Entwickelung des Amnion, Wolff'schen Ganges und der Allantois bei den Reptilien. (Auszug aus d. Ungarischen. M. tud. akademiai Ertesitö''. 1888.) Zool. Anzeig., Bd. XI. pp. 138–141. 19 März, 1888.

89. Amnion und Wolff'sher Gang bei den Eidechsen. Math. u. naturw. Ber. aus Ungarn, Bd. VI. pp. 14–26, Taf. II., III. 1889.

[Translated from Math. es Termeszettud. Ertesito'', Bd. VI.]

Pintner, Theodor.

'80. Untersuchungen über den Bau des Bandwurmkörpers mit besonderen Berücksichtigung der Tetrabothrien und Tetrarhynchen. Arb. zool. Inst. Univ. Wien, Tom. III. Heft 2, pp. 163–242, 9 Holzschn., Taf. XIV.–XVIII. 1880.

Rabl, Carl.

'88. Ueber die Bildung des Mesoderms. Vortrag in der 3ten Sitz. d. Anat. Gesellsch. auf der 2ten Versamml. in Würzburg. Anat. Anzeig., Bd. III. pp. 667–673, 8 Abbild. [Diskussion, pp. 673–679.] 15 Aug., 1888.

Remak, Robert.

'55. Untersuchungen über die Entwickelung der Wirbelthiere. vi + xxxviii + 195 pp., 12 Taf. Berlin: Reimer. 1855.

Renson, George.

'83. Contributions à l'embryologie des organes d'excrétion des oiseaux et des Mammifères. Thèse Bruxelles. 56 pp., 3 Pl. Bruxelles: Mayolez. 1883.

Rolph, W.

'76. Untersuchungen über den Bau des Amphioxus lanceolatus. Morph. Jahrb., Bd. II. pp. 87–164, Taf. V.–VII. 1876.

Romiti.

'74. Ueber den Bau und die Entwickelung des Eierstockes und des Wolff'schen Ganges. Arch. f. mikr. Anat., Bd. X. pp. 200–207, Taf. XIII. 1874.

Rosenberg, Alexander.

'67. Untersuchungen über die Entwicklung der Teleostier-Niere. Inaug. Diss. Dorpat. 77 pp., 1 Taf. Dorpat. 1867.

Roule, Louis.

'89. Études sur le développement des Annelides et un particulier d'un Oligochæte limicole marin (*Euchætræoides Marioni* nov. sp.). Ann. Sci. Nat., Sér. 7, Zool., Tom. VII. pp. 107–422, Pl. VIII.–XXII., 22 Fig. dans le Texte. 1889.

Rückert, Johannes.

'88. Ueber die Entstehung der Excretionsorgane bei Selachiern. Arch. f. Anat. u. Physiol., Jahrg. 1888, Anat. Abt., pp. 205–278, Taf. XIV.–XVI. 15 June, 1888.

'89. Zur Entwicklung des Excretionssystem der Selachier. Eine Erwiderung an Herrn van Wijhe. Zool. Anzeig., Bd. XII. pp. 15–22. 7 Jan., 1889.

Rückert, Joh., und W. Mollier.

'89. Ueber die Entstehung des Vornierensystems bei Triton, Rana, und Bufo. Sitz.-Ber. Gesellsch. f. Morph. u. Physiol. in München, Bd. V. Heft 2, pp. 47, 48. 1889.

Ryder, John A.

'87. [Résumé of Haddon ('87).] Amer. Naturalist, Vol. XXI. pp. 587–590. June, 1887.

Salensky, V.

'78, '80. Исторія развитія стерляди (Acipenser ruthenus). Труды Общества Естествоиспытателей при ИМП. Казан. Унив. Т. VII., вып. 2, 3, стр. 1–545, Таб. I.–XIX. Казань. 1878, 1880.

[History of the Development of the Sterlet (Acipenser ruthenus). Mem. Soc. Naturalists Imp. Univ. Kasan, Vol. VII. No. 2, 3, pp. 1–545, Pl. I.–XIX. Kasan. 1878, 1880.]

'81. Recherches sur le développement du Sterlet (Acipenser ruthenus). Arch. de Biol., Tom. II. Fasc. 2, pp. 233–341, Pl. XV.–XVIII. 1881. [Author's abstract of V. Salensky, '78, '80.]

Schmiegelow, E.

'81. Studier over Testis og Epididymis Udviklingshistorie. 96 Sid., 3 Taf. (Afhandl. for Doctors-graden.) Kjobenhavn. 1881.

'82. Studien über die Entwickelung des Hodens und des Nebenhodens. Arch. f. Anat. und Physiol., Jahrg. 1882, Anat. Abt., pp. 157–168, Taf. X., 1 Holzschn. 9 Aug., 1882.

Schultz, Alexander.

'75. Zur Entwickelung des Selachiereies. Arch. f. mikr. Anat., Bd. XI. pp. 569–582, Taf. XXXIV. 1875.

Schultze, Oscar.

'88. Die Entwickelung der Keimblätter und der Chorda dorsalis von Rana fusca. Zeitschr. f. wiss. Zool., Bd. XLVII. pp. 325–352, Taf. XXVIII., XXIX. 27 Nov., 1888.

Scott, W. B.

'81. Beiträge zur Entwickelung der Petromyzonten. Morph. Jahrb., Bd. VII. pp. 101–172, Taf. VII.–XI. 1881.

Sedgwick, Adam.

'80ª. Development of the Kidney in relation to the Wolffian Body in the Chick. Quart. Jour. Micr. Sci., Vol. XX. pp. 62–83, Pl. VI., VII. April, 1880.

[*Also in* Stud. Morph. Lab. Univ. Cambridge, Vol. I.]

'80ᵇ. On the Development of the Structure known as the Glomerulus of the Head-Kidney in the Chick. Quart. Jour. Micr. Sci., Vol. XX. pp. 372–374. July, 1880.

'81. On the Early Development of the Anterior Part of the Wolffian Duct and Body in the Chick, together with some Remarks on the Excretory System of the Vertebrata. Quart. Jour. Micr. Sci., Vol. XXI. pp. 432–468, Pl. XXVI. July, 1881.

Selenka, Emil.

'82. Der embryonale Excretions apparat des kiemenlosen Hylodes martinicensis. Sitz.-Ber. d. k. Akad. Wiss. Berlin. No. 8, Sitz. v. 16. Feb., 1882, pp. 117–124, Taf. II. 1882.

Semon, Richard.

'90. Ueber die morphologische Bedeutung der Urniere in ihrem Verhältnis zur Vorniere und Nebenniere und über ihre Verbindung mit dem Genitalsystem. Anat. Anzeig., Bd. V. pp. 455–482, 8 Abbild. 22 Aug., 1890.

[Im Auszuge mitgetheilt *in* Verhandl. d. X. internat. medic. Kongresses, Berlin, 1890, Bd. II. Abt. 1, Anatomie, pp. 135, 136. Diskussion: Wiedersheim, Semon. April, 1891.]

Semper, Carl.

'74. Die Stammesverwandtschaft der Wirbelthiere und Wirbelosen. Arb. zool.-zoot. Inst. Würzburg, Bd. II. pp. 25–76, Taf. III.–V., 1 Zylogr. 1874.

'75. Das Urogenitalsystem der Plagiostomen und seine Bedeutung für das der übrigen Wirbelthiere. Arb. zool.-zoot. Inst. Würzburg, Bd. II. pp. 195–509, Taf. X.–XXII. 1875.

'76. Die Verwandtschaftsbeziehungen der gegliederten Thiere. III. Strobilation und Segmentation (nebst einen Anhang). Arb. zool.-zoot. Inst. Würzburg, Bd. III. pp. 114–404, Taf. V.–XV. 15 Oct., 1876.

'78. Sind die Segmentalorgane der Anneliden homolog mit denen der Wirbelthiere? Eine Erwiderung an Herrn Dr. Fürbringer. Morph. Jahrb., Bd. IV. pp. 322–327. 1878.

Shipley, Arthur E.

'87. On Some Points in the Development of Petromyzon fluviatilis. Quart. Jour. Micr. Sci., Vol. XXVII. pp. 325–370, Pl. XXVI.–XXIX. Jan., 1887.

[*Also in* Stud. Morph. Lab. Univ. Cambridge, Vol. III. pp. 173–218.]

Siemerling, Ernst.

'82. Beiträge zur Embryologie der Excretionsorgane des Vogels. Inaug. Diss. Marburg. 40 pp., 1 Taf. Marburg. 1882.

Spee, Ferdinand Graf.

'84. Ueber direkte Betheiligung, des Ektodermes an der Bildung der Urnierenanlage des Meerschweinchens. Arch. f. Anat. u. Physiol., Jahrg. 1884, Anat. Abt., pp. 89–102, Taf. V. 7 März, 1884.

'86. Ueber weitere Befunde zur Entwickelung der Urniere. Mitth. Ver. Schlesw.-Holst. Aerzte, Heft 11, Stück 2, 2 pp. Kiel. 1886.

Spengel, J. W.

'76. Das Urogenitalsystem der Amphibien. Arb. zool.-zoot. Inst. Würzburg, Bd. III., Heft 1, pp. 1–114, Taf. I.–IV. 1 Juli, 1876.

'90. Beitrag zur Kenntniss der Kiemen des Amphioxus. Zool. Jahrbücher, Abt. f. Anat. u. Ontog., Bd. IV. Heft 2, pp. 257–296, Taf. XVII., XVIII. 30 Sept., 1890.

Spoof, A. A.

'83. Beiträge zur Embryologie und vergleichenden Anatomie der Cloake und der Urogenitalorgane bei den höheren Wirbelthieren. Akad. Habil.-Schr. Helsingfors. xix + 116 pp., 5 Taf. Helsingfors. 1883.

Strahl, H.

'86. Ueber den Wolff'schen Gang und die Segmentalbläschen bei Lacerta. Sitz.-Ber. naturf. Gesellsch. Marburg, Jahrg. 1886, Nro. 3, pp. 46, 47. Aug., 1886.

Strahl, H., und E. Martin.

'86. Anlage des Wolff'schen Ganges beim Kaninchen. Sitz.-Ber. naturf. Gesellsch. Marburg, Jahrg. 1886, Nro. 3, pp. 46, 47. Aug., 1886.

Sutton, J. Bland.

'86. An Introduction to General Pathology. xvi + 390 pp., 149 Figs. Philadelphia: Blakiston. 1889.

Timm, R.

'83. Beobachtungen über Phreoryctis Menkeanus Hoffm. und Nais, ein Beitrag zur Kenntniss der Fauna Unterfrankens. Arb. zool.-zoot. Inst. Würzburg, Bd. VI. pp. 109–157, Taf. X., XI. 1883.

Veith.

'89. Vaginalepithel und Vaginaldrusen. Virch. Arch. f. path. Anat., Bd. CXVII. pp. 171–192, Taf. VII. 1 Juli, 1889.

Waldeyer, Wilhelm.

'70. Eierstock und Ei. Ein Beiträg zur Anatomie und Entwickelungsgeschichte der Sexualorgane. viii + 174 pp., 6 Taf. Leipzig: Engelmann. 1870.

Weiss, F. Ernest.

'90. Excretory Tubules in Amphioxus. Quart. Jour. Micr. Sci., Vol. XXXI. pp. 489–497, Pl. XXXIV., XXXV. Nov., 1890.

Weldon, W. F. R.

'83. Note on the Early Development of Lacerta. Quart. Jour. Micr. Sci., Vol. XXIII. pp. 134–144, Pl. IV.–VI. 1883.

'84. On the Head-Kidney of Bdellostoma, with a Suggestion as to the Origin of the Suprarenal Bodies. Quart. Jour. Micr. Sci., Vol. XXIV. pp. 171–182, Pl. XV. April, 1884.

Wichmann, Ralf.

'84. Beiträge zur Kenntniss des Baues und der Entwicklung der Nierenorgane der Batrachier. Inaug. Diss. Bonn. 20 pp. Bonn: Georgi. 1884.

Wiedersheim, Robert

'86 Lehrbuch der vergleichenden Anatomie der Wirbelthiere. 2te Auflage. xiv + 890 pp., 614 Figs. Jena: Fischer. 1886.

'90ª. Ueber die Entwicklung des Urogenitalapparates bei Krokodilen und Schildkröten. Anat. Anzeig., Bd. V. pp. 337–344. 5 Juli, 1890.

'90ᵇ. Ueber die Entwicklung des Urogenitalapparates bei Crocodilen und Schildkröten. Arch. f. mikr. Anat., Bd. XXXVI. pp. 410–468, Taf. XVI.–XVIII., 2 Holzschn. 22 Oct., 1890.

Wijhe, J. W. van.

'86. Die Betheiligung des Ektoderms an der Entwicklung des Vornierenganges. Zool. Anzeig., Bd. IX. pp. 633–635. 1 Nov., 1886.

'87. Ontwikkeling van de uitscheidingsorganen der Selachiers. Nederl. Staatscourant, Oktobernummer. 1887.

'88ª. Ueber die Entwickelung des Excretionssystems und anderer Organe bei den Selachiern. Anat. Anzeig., Bd. III. pp. 74–76. 18 Jan., 1888.

'88ᵇ. Bemerkung zu Dr. Rückerts Artikel über die Entstehung der Excretionsorgane bei Selachiern. Zool. Anzeig., Bd. XI. pp. 539, 540. 1 Oct., 1888.

'89. Ueber die Mesodermsegmente des Rumpfes und die Entwicklung des Excretionssystems bei Selachiern. Arch. f. mikr. Anat., Bd. XXXIII. pp. 461–516, Taf. XXX.–XXXII. 25 Juli, 1889.

Wilson, Edmund B.

'87. The Germ-Bands of Lumbricus. Jour. of Morph., Vol. I. pp. 183–192, Pl. VII. Sept., 1887.

'89. The Embryology of the Earthworm. Jour. of Morph., Vol. III. pp. 387–462, Pl. XVI.–XXII. Dec., 1889.

Wilson, Henry V.

'90. On the Development of the Sea Bass (Serranus atrarius). Prelim. Comm. Johns Hopkins Univ. Circ., Vol. IX. No. 80, pp. 56–59, Figs. 3–5. April, 1890.

Wittich, von.

'52. Beiträge zur morphologischen und histologischen Entwickelung, der Harn- und Geschlechtswerkzeuge der nackten Amphibien. Zeitschr. f wiss. Zool., Bd. IV. pp. 125–167, Taf. X., XI. 2 Sept., 1852.

Ziegler, H. Ernst.

'87. Die Entstehung des Blutes bei Knochenfischembryonen. Arch. f. mikr. Anat., Bd. XXX. pp. 596–665, Taf. XXXVI.–XXXVIII. 18 Nov., 1887.

'88. Der Ursprung der mesenchymatischen Gewebe bei den Selachiern. Arch. f. mikr. Anat., Bd. XXXII. pp. 378–400, Taf. XIII. 17 Oct., 1888.

Zschokke, F.

'87. Studien über den anatomischen und histologischen Bau der Cestoden. Centralbl. f. Bakt. u. Parasitenk., Bd. I. pp. 161–165, 193–199. 1887.

EXPLANATION OF FIGURES.

All the Figures, unless otherwise stated, were drawn with the aid of an Abbé camera lucida, and represent the appearance of the *anterior* faces of the sections. Plates I.–IV. were made from preparations of Rana sylvatica Le Conte; Plates V.–VIII. from Rana sylvatica Le Conte, Bufo americanus Le Conte, and Amblystoma punctatum Linn.

ABBREVIATIONS.

(For the meaning of letters *a*, *b*, *c*, *d*, *e*, *f*, in Figures 24–26, see the explanation of those Figures.)

ao.	Aorta.
can. comn.	Communicating canal.
cd. spi.	Spinal cord.
cl. ms'drm.	Mesodermal cells.
cl. vt.	Yolk cells.
clo.	Cloaca.
cœl.	Cœlom.
cœl.'	Protovertebral cavity.
cœl.''	Body cavity.
cp. sng.	Blood cells.
cps. pr'nph.	Pronephric capsule.
cras. gn.	Ganglionic thickening.
cras. pr'nph.	Pronephric thickening.
cras. so'plu.	Somatopleural thickening.
d.	Dorsal aspect.
dt. sg.	Segmental duct.
dt. Cuv.	Ductus Cuvieri.
dx.	Right side.
ec'drm.	Ectoderm.
ec'drm.'	Superficial layer of same.
ec'drm.''	Deep layer of ectoderm.
en'th.	Endothelium.
fnd. arc. vr.	Deep layer of a vertebral arch.
fnd. cps.	Fundament of the pronephric capsule.
fnd. dt. sg.	Fundament of the segmental duct.
fnd. glm.	Fundament of the glomus.
fnd. glm.'	Fundament of glomerulus.
fnd. gn. spi.	Fundament of a spinal ganglion.
fnd. mbm.	Limb bud.
fnd. ms'nph.	Fundaments of mesonephric tubules.
fnd. nph'st.$^{\mathrm{I}}$	Fundament of first pronephric nephrostome.
fnd. pul.	Lung bud.
glm.	Glomus.
gn. nd.	Ganglion nodosum.
gn. spi.	Spinal ganglion.
hp.	Liver.
in.	Intestine.
la. l.	Lateral plate.
la. med.	Medullary plate.
la. ms'drm.	Mesodermal plate.
la. pi'ton.	Peritoneal layer.
la. pr'vr.	Protovertebral plate.
la. so.	Somatic layer.
la. spl.	Splanchnic layer.
m.	Median.
mb. ba.	Basement membrane.
ms'drm.	Mesoderm.
ms'chy.	Mesenchyme.
my'tm.	Myotome.
n. l.	Nervus lateralis.
n'cd.	Chorda dorsalis.
nph'stm.	Nephrostome.
nph'stm.$^{\mathrm{I., II., III.}}$	1st, 2d, and 3d pronephric nephrostome, respectively.
pi'ton.	Peritoneum.
pr'vr.	Protovertebra.
rx. ao.	Aortic root.
rx. vag.	Root of the vagus nerve.
sb.-n'cd.	Sub-notochordal rod.
sn. sng.	Blood sinus.
so.$^{\mathrm{I., II.,}}$ etc.	Somites I., II., etc.
so'plu.	Somatopleure.
sph. vt.	Yolk spherules.
spl'plu.	Splanchnopleure.
tbl. nph'stm.$^{\mathrm{I., II., III.}}$	1st, 2d, and 3d nephrostomal tubules respectively.
tbl. pr'nph.	Pronephric tubule.
trn. clg.	Collecting trunk.
trn. com.	Common trunk.
va. sng.	Blood-vessel.
vn. crd.	Posterior cardinal vein.
vn. jgl.	Jugular vein.

PLATE I.

Fig. 1. A portion of a cross section through the anterior trunk region of one of the older embryos included under Stage I. × 110.

" 2. A cross section through the same embryo in the middle trunk region. × 25.

" 3. A portion of a cross section through the middle trunk region of one of the younger embryos in Stage I. × 92.

" 4. A portion of a cross section through the hinder trunk region of one of the younger embryos belonging to Stage II. × 92.

" 5. A portion of a cross section through the anterior trunk region of one of the older embryos from Stage II. The section passes through an interprotovertebral septum. × 110.

" 6. A portion of a cross section from one of the older embryos in Stage III. The plane of the section passes through the middle of Somite III. × 110.

" 7. A small segment of a cross section through the embryo shown in Figures 15–17 of Plate II. The Figure represents a portion of the ventrolateral ectoderm with three subjacent mesodermal cells. × 615.

" 8. A portion of a cross section through the embryo shown in Figures 18–22, Plate III. It shows the fundament of the glomus. × 110.

" 9. A portion of a cross section through a slightly older embryo, showing the glomus in a more advanced stage of development. × 110.

" 10. A portion of a cross section through an embryo of Stage V., showing a branch of the aorta which gives off a small vessel to the glomus. × 150.

B.Meisel, lith. Boston

PLATE II.

All the Figures on this plate are magnified 110 diameters.

Figs 11 and 12. Portions of two frontal sections through the pronephric thickening of one of the older embryos belonging to Stage III.

Fig. 11 shows the dorsal margin of the thickening.

Fig. 12 shows a section through the nephrostomal region.

Figs. 13 and 14. Portions of two frontal sections from one of the younger embryos of Stage II.

Fig. 13 shows the ventral ends of the anterior protovertebræ.

Fig. 14 shows a section through the dorsal portion of the pronephric thickening.

Figs. 15–17. Portions of three cross sections through one of the younger embryos of Stage III.

Fig. 15 shows the anterior end of the pronephric thickening. The plane of the section passes a little behind the middle of Somite II.

Fig. 16 shows the pronephric thickening in the region of Somite V.

Fig. 17 shows the thickening near its posterior termination.

PLATE III.

Figures 18–22 and 27 are magnified 110 diameters; Figures 23–26, 260 diameters.

Figs. 18–22. Portions of a series of cross sections through an embryo of Stage IV. In Figure 18, the pronephros of the right side is shown; in the remaining Figures, the pronephric organs of the left side. The location of the several sections on the reconstruction (Fig. 39) is shown by the series of lines bearing corresponding numbers.

Fig. 18 shows the first nephrostome.

Fig. 19 is from a region between the first and the second nephrostomes.

Fig. 20 shows the second nephrostome.

Fig. 21 shows the third nephrostome and the anterior portion of the segmental duct.

Fig. 22 shows the segmental duct in the middle trunk region.

Figs. 23–26. Cross sections of the fundament of the segmental duct near its posterior termination, from an embryo of Stage IV.

Fig. 23 shows the duct five sections in front of its termination.

Fig. 24, three sections before its termination; *a.*, *b.*, and *c.*, cells in the fundament of the duct; *cd.*, portions of the two cells *c.* and *d.*, which are to be seen in the following section.

Fig. 25 shows the duct one section in front of its termination; *c.* and *d.*, cells in the rudiment of the duct; *b.* and *c.*, portions of two cells bearing the same lettering in Figure 24.

Fig. 26 shows the depression of the somatopleure (*f.*) directly behind the tip of the fundament of the duct.

Fig. 27. A cross section from a larva whose pronephros is shown in Figure 41. It shows the opening of the segmental duct into the cloaca.

27

nm
p.a.mbr
cœl''
ch
endm.
ec.dm
pal cp

26

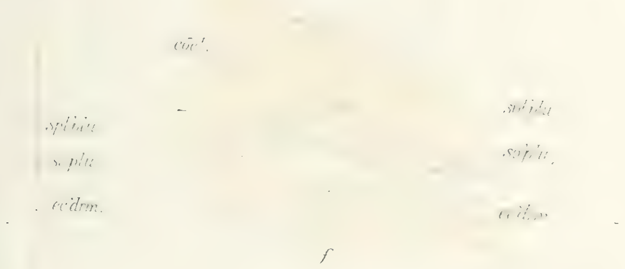
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PLATE IV.

Fig. 28. Part of a cross section through the anterior trunk region of a larva belonging to Stage VI. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 29. Part of an oblique longitudinal section through a larva of Stage IV. The plane of the section was directed so as to cut the somatopleure tangentially along the line of the three nephrostomes. Its direction is represented by the line 40 in Figure 20. × 110.

Fig. 30. Part of a cross section through the middle trunk region of a larva, from which Figure 28 was also drawn. (Stage VI.) × 110.

Fig. 31–38. A series of diagrams illustrating the convolution of the pronephric tubules. These diagrams, which are based upon reconstructions from cross sections, merely serve to show the number and approximate location of the loops in a longitudinal direction. No attempt has been made to indicate in the diagrams the changes in position undergone by the tubules in a transverse direction. The gray tint represents the common trunk and the anterior portion of the segmental duct. The first nephrostomal tubule and the collecting trunk are colored pink. The second and third tubules are represented in yellow and orange respectively.

Figs. 31–34 are from various larvæ of Stage V.

Fig. 32 is a diagram of the reconstruction shown in Figure 40.

Figs 33 and 34 represent the right and the left pronephros respectively of the same individual.

Figs. 35–37 are from various larvæ of Stage VI.

Fig. 36 is a diagram of the reconstruction shown in Figure 41.

Fig. 38 is from a larva of Rana halesina.

Figs. 39–41. A series of reconstructions from cross sections of larvæ in different stages of development. In Figures 40 and 41, the common trunk and the anterior portion of the segmental duct have been shaded without color; the collecting trunk and the first nephrostomal tubule have been colored pink; and the second and third nephrostomal tubules are respectively yellow and orange. × 65.

Fig. 39. Right pronephric pouch of a larva belonging to Stage IV., viewed from the median side. The ×'s represent the position of the nephrostomes. The lines 18–21 show the various levels at which the sections represented in Figures 18–21 were made.

Fig. 40. Right pronephros of a larva belonging to Stage V., viewed from the median side.

Fig. 41. Right pronephros of a larva belonging to Stage VI., viewed from the ventral side, the external face being uppermost.

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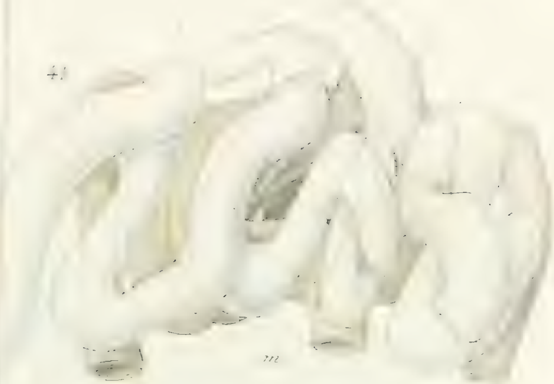

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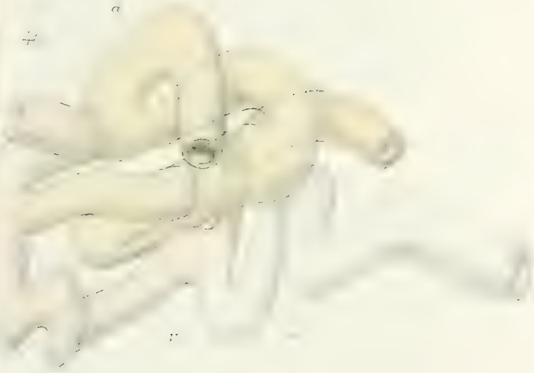

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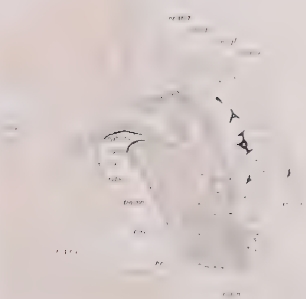

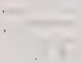

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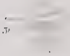

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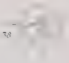

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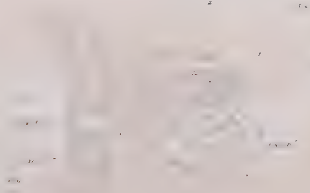

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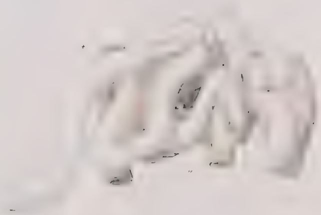

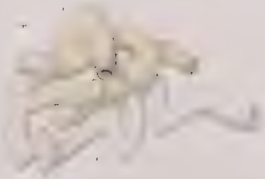

PLATE V.

Fig. 42. A portion of a cross section through the anterior trunk region of a larva of Bufo, belonging to Stage V. The Figure shows the pronephros in the region of the first nephrostome. × 110.

Fig. 43. A section through the rudiment of the duct near its hinder tip, from an embryo of Bufo belonging to Stage IV. × 500. Zeiss apochr. 4 mm. Oc. B.

Fig. 44. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The section shows the pronephric thickening in the region of its greatest development. × 65.

Fig. 45. A portion of a cross section through the anterior trunk region of an embryo of Rana belonging to Stage IV. The section shows the pronephric pouch in the region of the second nephrostome. × 110.

Fig. 46. An embryonic blood corpuscle occurring in the glomus of a larva of Bufo belonging to Stage V. × 955.

.-PRONEPHROS IN AMPHIBIA

PL. V

[illegible]

PLATE VI.

Fig. 47. A portion of a cross section through the anterior trunk region of a larva of Bufo belonging to Stage V. The Figure shows the pronephric structures in a region between the first and second nephrostomes. × 158.

Fig. 48. A portion of a cross section through the middle trunk region of an embryo of Amblystoma belonging to Stage I. × 65.

Fig. 49. Anterior face of a cross section through the glomus of a larva of Bufo belonging to Stage V. × 470. Zeiss apocr. 4 mm. Oc. 6.

Fig. 50. Anterior face of a portion of a cross section through the right glomus of the same larva, including also the opposite peritoneal wall. × 710. Zeiss apochr. 4 mm. Oc. 12.

Fig. 51. A cross section (right side, anterior face) through the pronephros represented in Figure 37. The section passes directly in front of the third nephrostome, and shows the expanded region of the common trunk at the level of its union with the collecting trunk. × 90.

Fig. 52. A portion of a cross section through the glomus of a larva of Bufo belonging to Stage V. The Figure shows an infolding (opposite the letters *cœl.″*) of the outer peritoneal layer of the glomus. × 500.

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PLATE VII.

Fig. 53. A portion of a cross section through the posterior trunk region of a larva of Amblystoma belonging to Stage VI. The section shows the fundament of the second primary mesonephric tubule (*dt. sp.*). × 90.

Fig. 54. A portion of a cross section through the middle trunk region of a larva of Amblystoma belonging to Stage VI. The section shows one of the " cords of cells " which occur between the mesonephros and the pronephros ; it exhibits a case of nuclear mitosis in the peritoneum, which suggests the origin of these cells. × 500. Zeiss apochr. 4 mm. Oc. 8.

Fig. 55. A portion of a cross section through the anterior trunk region of an embryo of Amblystoma belonging to Stage III. The pronephric thickening is shown in the region of the middle of Somite II. × 90.

Fig. 56. A portion of a cross section from the same series. The pronephric thickening is shown in the region of the posterior face of Somite II. × 90.

Fid. ad nat.

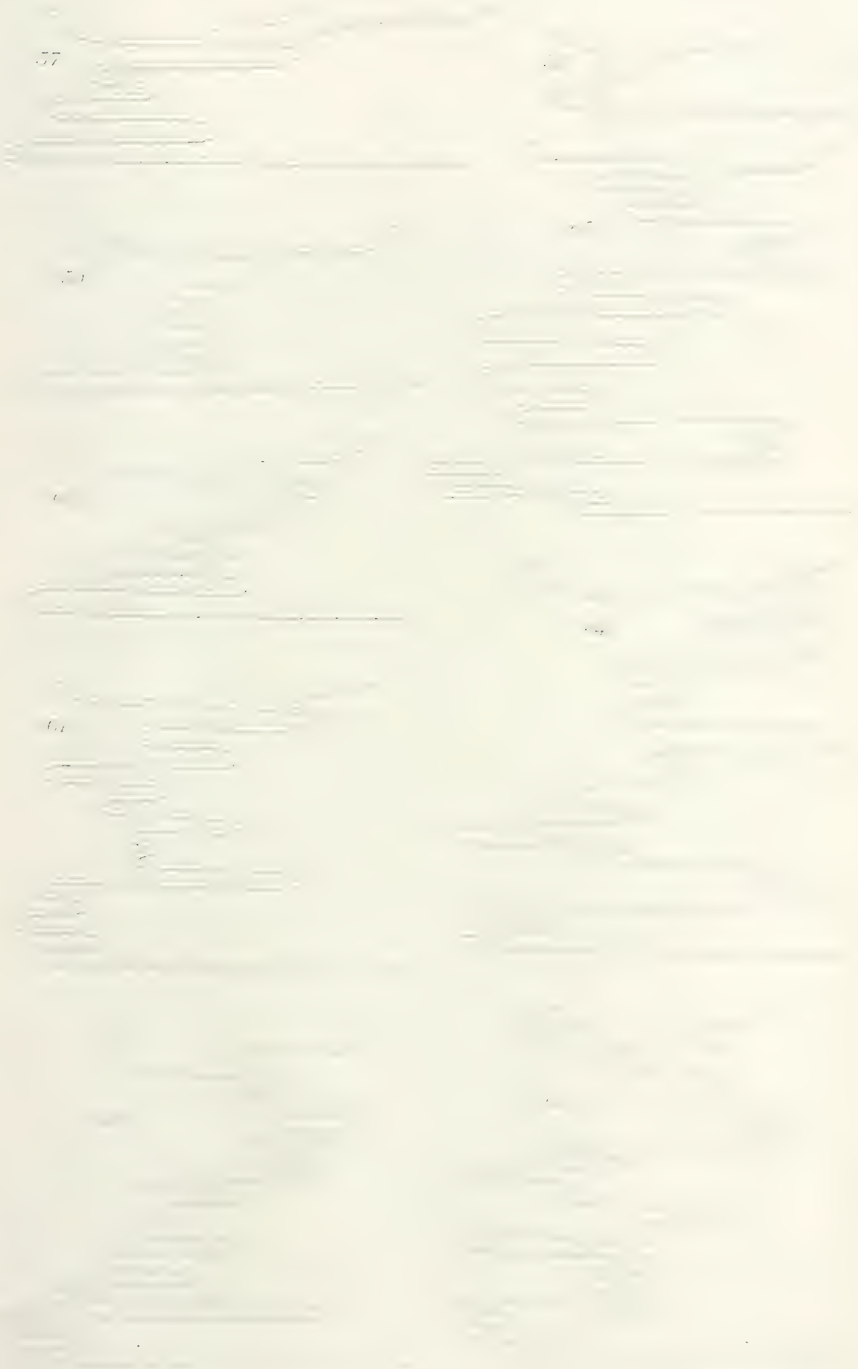
B. Meisel lith. Boston

PLATE VIII.

Figs. 57–60. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage V.

Fig. 57. Reconstruction of a pronephros showing three nephrostomal tubules.

Figs. 61–65. Reconstructions of several pronephridia of Amblystoma larvæ belonging to Stage VI.



BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE.

VOL. XXII.

CAMBRIDGE, MASS., U. S. A.
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No. 1. — *Observations on Budding in Paludicella and some other Bryozoa.* By C. B. Davenport.[1]

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A. SPECIAL PART.

I. Introduction.

The somewhat heterogeneous studies here brought together have been prosecuted at different times and in different places, as opportunity for getting light on the problem of non-sexual reproduction as exhibited in the group of Bryozoa has presented itself.

While studies on the fresh water species were pursued chiefly here at Cambridge, those on marine Bryozoa were made while occupying one of the tables of the Museum at the United States Fish Commission Laboratory at Wood's Holl, Mass., during the summer of 1889, and while at Mr Agassiz's Newport Laboratory during the summer of 1890. To my instructor, Dr. E. L. Mark, for many valuable suggestions during the progress of my work and the writing of this paper, to Mr. Alexander Agassiz, for the kind hospitality accorded me at his Newport Laboratory, and to Hon. Marshall McDonald, United States Commissioner of Fish and Fisheries, and Dr. H. V. Wilson, Assistant at Wood's Holl, for favors shown me while at the Wood's Holl Laboratory, I make grateful acknowledgment of my indebtedness.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXVIII.

A word as to localities. The marine Bryozoa were found especially abundant at Newport on floating eel-grass in the cove and on the piles of the wharf. The embryos of Cristatella and Plumatella were found in colonies which literally covered the bottom of some parts of the south or shady side of Trinity Lake, Pound Ridge, New York. They occur especially in densely shaded and fairly deep water near the shore.

The Gymnolæmata present many difficulties to finer technique. They possess a chitinous covering, often very thick, and frequently, in addition, a calcarous skeleton. When the latter is present, picro-nitric acid mixed with sea water is a fairly good fixing reagent; when it is absent, hot corrosive sublimate was most serviceable. The objects must be transferred through the grades of alcohol with extreme caution, to prevent the collapse of the ectocyst. I used the chloroform-paraffin method of embedding in order to make transfers more gradual at this stage. Some difficulty was experienced in staining such small objects on the slide, since the tissues are very loosely associated; and on the other hand *in toto* staining is unsatisfactory in some cases, owing to impenetrability of the ectocyst. Often it was necessary to open the body cavity of each individual by means of a sharp knife or needle. The best results were obtained with alcoholic dyes like Kleinenberg's hæmatoxylin and Mayer's cochineal; although Ehrlich's hæmatoxylin was often used with success.

II. Budding in Paludicella.

1. Architecture of the Stock.

Paludicella, as is well known, occurs in quiet streams and forms stocks on the under surfaces of stones and other objects. Seen with the naked eye these stocks appear as a fine lacework, composed of constantly branching lines of individuals. Some of the stocks which I have measured are over 25 mm. in length along their greatest diameter.

When the stock is studied more carefully, it is seen that the individuals which compose it are arranged one in front of the other, forming lines. (Figs. 1, 2, 2ᵃ.) We may distinguish (1) a single primary branch, which forms a continuous line from the oldest individual, which has been derived directly from the egg, to the terminal one; and (2) secondary branches, which arise from the individuals of the primary branch and at right angles to their axes. Typically, a secondary branch arises from both the right and left sides of each adult member of the primary branch, but in some cases the secondary branch of only one side appears to be formed. The secondary branches are composed, like the primary, of a continuous line of individuals placed end to end. These in turn give rise to tertiary branches, which run out at right angles to the right and to the left of the secondary ones, and hence parallel to the primary branches. Quaternary branches may occur in like manner, but I have never seen branches of a higher order than the fourth. All of these branches may lie in one plane, but frequently some of the lateral buds are so placed that they give origin to secondary branches which rise above the plane of the object upon which the stock lies. A study of Figure 1 and the corresponding diagram, Figure 2, reveals some additional facts. The two lateral buds of an individual do not arise at the same time, and there is a tendency for the first, and therefore oldest and most developed, secondary branches to arise alternately on opposite sides of the primary branch. This last rule has many exceptions, however.

The long axis of the individual coincides with that of its branch; the sagittal plane lies in that axis, and at right angles to the substratum. The atrial opening is near the distal end of the individual in the sagittal plane, and is turned away from the substratum. The anal aspect of the polypide is placed nearer the tip of the branch, — hence distad; the mouth, on the contrary, proximad.

A very casual observation shows that not all branches nor all individuals are of the same size. The shortest and therefore youngest branches are placed most distally, and are seen as small buds. The terminal individuals of the branches are also evidently less well developed than the more proximal ones. The adult individuals measure from 1.5 to 2.0 mm. in length and from 0.30 to 0.35 mm. in width. The younger individuals differ from the older in form also. The outline of the adult branch, looked at from the side, and disregarding the atrial opening, is formed by a series of beautiful sigmoid curves (Fig. 9). The concave and convex points of the upper and lower sides of an individual are not placed exactly opposite each other, and the lower (abatrial) side approximates more nearly to a straight line. The point at which the upper and lower curves most nearly approach each other is where the separation of two individuals takes place; that at which they are farthest apart is the middle of the zoœcium, occupied by the polypide and sexual organs. The outlines of the young zoœcia are straighter, and their breadth is considerably less than that of the adult.

From what we have already seen, the method of growth of the stock is perfectly evident: it is by the formation of new median buds at the tips of existing branches, and of new branches from lateral buds. In order to understand the origin of the individuals of the primary branches, to which subject we will first turn our attention, we must study the tips of the branches.

2. HISTOLOGY OF THE BUDDING REGION.

Figures 7–9 will serve to show more in detail the method of formation of new terminal individuals. We find in these cases one polypide already pretty well developed and attached to the body wall by means of the kamptoderm at about the point at which the pyramidal muscles (*mu. pyr.*) are seen to be forming. That portion of the animal which extends from about the region of formation of the muscles to a point a little proximad of the tip represents the region which will go to form the new individual. The tip itself, for reasons which will presently appear, is not to be included in the terminal individual. The tip of the branch is to be regarded as homologous with the margin of the corm in corm-building genera of Gymnolæmata. Figures 7–9 (*gn.*) also show the position of the bud which is to produce the polypide. By consulting first Figure 9, in which the polypide bud is apparent, the significance of the swellings of the body wall in Figures 8 and 7 becomes clear.

Figure 14 (Plate II.) represents a stage in the development of the polypide bud, somewhat later than that shown in Figure 9, and this may serve us as a starting point in our study of the origin of a new individual, and, first of all, of the new polypide. The whole of Figure 14, from the tip down to the neck of the older polypide (*cev. pyd.*), may be divided, for convenience, into three zones: first, that distad of the young bud, which may be called the *tip of the branch* (Fig. 14, α to β); secondly, the region of the bud itself, which may be called the *gemmiparous zone* (β to γ); and thirdly, the region between this last zone and the neck of the older polypide, which, for want of a better name, may be called the *proximal zone* (γ to δ). In the formation of a new polypide between α and β, that region will in turn become divisible into the three zones just named, exactly as the region *a* to *δ* represented the *tip* of the branch when the older polypide, whose neck is shown at *cev. pyd.*, was of the age that the younger bud is now. It will be necessary first of all to study carefully each of these three regions before treating of their origin and fate.

The *tip of the branch* consists of the two layers of cells which are found in other parts of the body wall, — the ectoderm and the mesoderm, as the cœlomic epithelium may, for brevity's sake, be called. The cells of the ectoderm at the extreme tip (Plate I. Fig. 6) are greatly elongated, forming a columnar epithelium. There are about 25 or 30 of the larger cells. They have a length of 28 μ to 32 μ, and a diameter of about 4 μ. They possess an ovoid nucleus averaging 5.7 μ by 2.6 μ, which lies in the middle of the cell but slightly nearer the cœlomic epithelium than the cuticula. It possesses a large nucleolus over 1 μ in diameter, which often appears stellate owing to the threads of plasma surrounding and proceeding from it and forming a nuclear network. As the figure shows, the plasma of the cell is filled with large, apparently deeply stained granules, some of the largest being over 0.6 μ in diameter. The coarser granules lie chiefly in the immediate vicinity of the nucleus, but are also found arranged in long lines at right angles to the surface throughout the greater part of the cell, becoming finer the farther they lie from the nucleus. A fine network can sometimes be made out between the large granules, but this appearance is more evident at the peripheral portion of the cell, where there are no large granules. At the outer and inner ends of the cells one finds large vacuoles, the largest of which are of about the same size as the nucleus; these become smaller the nearer they lie to the nucleus. In many cases the larger vacuoles are each seen to be partly filled by a body which stains slightly, and, as focusing determines, is more highly refractive than the plasma. Similar highly refracting, slightly staining granules are found in, and in fact often composing, the smaller "vacuoles." Owing to the fact that the deeply staining granules lie near the nuclei, and that the vacuolated and finely granular plasma lies more remote, there is a very marked deeply staining band occupying the middle of the ectodermal layer, and having about four tenths the thickness of the whole layer.

At the outer ends of the cells, and doubtless secreted by them, there is a cuticula about 1 μ thick. Its inner surface is sharply marked off from the underlying plasma; its outer surface is less sharp, and there are usually very minute particles of dirt attached to it (not represented in the figure). The whole cuticula forms in section a continuous band of substance, which stains deeply in Ehrlich's hæmatoxylin (but not at all in alum cochineal), and covers nearly the whole tip. Looked at from the surface after staining in hæmatoxylin, it appears uniformly dark. The mesoderm of the tip is highly modified, and a description of it will be more instructive after I shall have described the normal cœlomic epithelium, as I shall do later.

Passing from the extreme tip towards β (Fig. 14), one finds the ectodermal cells gradually changing in form, size, and structure, and becoming slightly broader, and very much shorter. Their nuclei lie near the inner ends of the cells, possess a thick "nuclear membrane," and are more nearly spherical than those of the columnar cells, but of about the same size. They each possess one very large, centrally placed nucleolus, whose diameter equals and sometimes exceeds one third that of the nucleus, and whose outline is often somewhat stellate. Outside of the nucleus in the cell body there are fewer and fewer vacuoles as we pass from the tip, but the plasma is still coarsely granular, and here, as before, these stained granules surround the nucleus. It is now the regions between cells rather than those at the inner and outer ends which remain unstained, so that the cells are separated from one another by light spaces.

The mesodermal layer becomes somewhat thinner than at the tip, that is to say, its cells are flattened. The nuclei are elongated in the axis of the branch, and average about $4\,\mu$ by $2.2\,\mu$. They possess one spherical nucleolus, whose diameter is about two thirds of the minor axis of the nucleus. Small, clear vacuoles often with highly refractive spherical bodies are abundant in the cell protoplasm, which stains as a whole less deeply than does the ectoderm. Such highly vacuolated elements will be called *reticulated cells.*

If we study the *gemmiparous zone* at a stage considerably earlier than that shown in Figure 14, in fact at a stage in which a polypide is about to arise, we find an appearance of the layers represented by Plate I. Fig. 3. In such a region the ectoderm consists of cuboid cells about $7\,\mu$ high by $6.5\,\mu$ broad. The nuclei are large, nearly spherical, and vary in size from $3.5\,\mu$ to $6.0\,\mu$. The largest nuclei are those in the region from which a bud is about to arise (*ex.*). One in this region (to the right of *ex.*) is $6.5\,\mu$ by $6.0\,\mu$ in diameter, with a nearly spherical, eccentrically placed nucleolus of about $3.0\,\mu$ in diameter. This nucleus is the largest which I have found in the whole tissue of Paludicella, and the same is true of the nucleolus. From the examination of many regions from which buds are about to arise, I can assert that such regions always, in Paludicella, possess large nuclei and large deeply staining nucleoli. I shall have occasion to describe similar conditions elsewhere, and to point out the probable significance of these facts. The cell body possesses a highly granular, deeply staining plasma; the inner ends of the cells, however, do not stain so deeply as the middle or peripheral portions.

The cuticula (omitted from Fig. 3, see Fig. 5) is usually somewhat different in appearance from that at the extreme tip. In section we can distinguish two layers: an outer, thicker, deeply staining layer, which is not continuous but appears broken into larger or smaller bits; and an inner, thin, non-stainable and highly refractive portion, from which the first layer is often slightly separated. This second layer is closely applied to the underlying cells, which doubtless secrete it. Looked at from the surface (Fig. 10, *a.*) the deeply stainable layer is seen to be broken into irregular polygonal pieces ranging from 2 μ to 17 μ in diameter and separated from one another by spaces ranging from 0 to 6 μ.

The mesoderm forms a loose epithelium, whose average width is less than that of the ectoderm (Fig. 3, *ms'drm.*). As a whole, moreover, it stains less deeply. In a portion of the gemmiparous zone, which lies about 180° from the budding region, the mesoderm has become so delicate a layer, if it exists at all, as not to be easily distinguishable. In the vicinity of the bud its cells have irregular outlines and extend out into the cœlom as though possessed of the power of amœboid movement. The nuclei are spherical or ovoid, smaller than those of the ectoderm, and on the whole have smaller nucleoli. The cell body is highly vacuolated. The vacuoles are not large and clear in outline, but whole regions of the cell body seem to be reduced to a non-stainable condition, and in some of these regions a fine network may still be observed.

The *proximal zone* (Fig. 14, γ to δ) is distinguished, soon after the first rudiment of the bud appears, by the diminished thickness of the ectoderm. The cells have become transformed from a columnar to a pavement epithelium. The nuclei are smaller, the nucleoli less prominent, and the cell body stains much less deeply. The cuticula is of two kinds, as before, but with this difference: the deeply staining outer part is less conspicuous, and the pieces are smaller and more widely separated. Looked at from the surface, we find an appearance like Figure 10, *c.*, in which the dark bodies represent the deeply staining cuticula. These pieces are much smaller than those of the gemmiparous zone, ranging from 0.6 μ to 9.5 μ in diameter, and separated from each other by spaces ranging from 0 to 13 μ.

3. ORIGIN OF THE POLYPIDE IN THE TERMINAL BUD.

Observation having shown that budding in Paludicella follows definite laws, we ought to be able to discover the place and time at which buds will arise ; and it is necessary to do this in order to study the origin of the gemmiparous cells, and the changes which they undergo preparatory to an actual involution.

The study of tips of branches shows that the necks of the polypides of any branch all lie in one plane, and that this plane also includes the youngest polypide ; also that the youngest polypides always arise distad of the next older. Knowing these facts, our observations may be confined to a short line running from the neck of the youngest apparent buds to the tips of the branches studied. The time at which to search for incipient buds and the place in the line where they will be found is illustrated by Figure 7 (Plate I.). The youngest *developed* bud is one the axes of whose tentacles are approximately parallel to the axis of the branch, and whose brain cavity, *gn.*, is not yet constricted off from that of the œsophagus. The place of origin is near the tip, immediately beyond the point at which the ectoderm changes rapidly from a columnar to a pavement epithelium.

Figure 3 is from a section across the branch in the region of an incipient bud. I have already described the conditions of the cells of this region. Those near *ex.* are larger than the surrounding ones, and show signs of cell division both in the ectoderm and mesoderm. In both cases shown in the figure, the direction of division is such as will tend to increase the superficial area of the layer in which it occurs. The ectoderm seems to be the most important layer of the two in the process of invagination which is about to take place. I think one is led to this conclusion if one considers a folding of an epithelium to be due to an increase in the area of the epithelium within a certain circumference without a correspondingly great increase in the circumference itself. Such a conception implies, first of all, mutual pressure of the cells of the invaginating epithelium. The cells of the mesodermal layer do not seem to be under mutual pressure ; in some cases they are barely in contact. The cells of the ectoderm are evidently closely applied, and probably, therefore, under mutual pressure.

The one case of cell division which is occurring in the ectoderm is at the inner end of the cell. In fact, the centre of the nuclear plate is much nearer the deep end than are the centres of the adjacent nuclei. The effect of this division is to increase the area on the inner surface of the ectoderm more than that on the outer, as appears from a study of the sections shown in Figures 4 and 5. In Figure 4 certain cells lie already below the *niveau* of the surrounding ones, very much as though they had moved downward on account of this being the direction of least resistance. A later stage of this process is shown in Figure 5. Here the nuclei are already arranged in a deep saucer-shaped layer. The transition to the U-shaped arrangement of Figure 37 (Plate IV.), in which the invagination of the inner layer of the bud is completed, is not a difficult one to understand. It is to be observed, however, that the folding is of such character that it can hardly be termed a typical invagination. Comparing Figures 4, 5, and 37, it appears rather to be of a type somewhat intermediate between typical invagination and typical ingression. The cavity of the bud first arises through a rearrangement and reshaping of the cells of the inner layer of the bud. At this stage the nuclei of the invaginated region stain very deeply, and have large nucleoli.

Figure 21 (Plate III.) shows the condition of the bud at this stage as seen in longitudinal section. The proliferation which gave rise to the rudiment of the bud is shown, by a comparison of Figures 37 and 21, not to have been confined to one point, but to have occurred along a line, so that the resulting bud is boat-shaped, and not cup-shaped. The whole mass is therefore bilaterally symmetrical. Even at this early stage one can distinguish a difference in the form of the bud at the anal and oral ends. At the oral end (*Or.*) the bud passes more abruptly into the body wall than at the anal end. Later, this feature becomes more marked. This is an indication of a fact for which later stages will bring better evidence: that the formation of the bud proceeds from the oral towards the anal end, and that the increased length of the bud that one finds in the stage represented by Figure 22 is due to growth at the anal end.

4. Origin and Development of the Lateral Branches.

The first lateral branch appears as a prominent protrusion of the lateral walls of an individual of the primary branch when the ganglion of that individual has already nearly closed, and when the bud of the next younger individual has attained a stage somewhat later than that shown in Figure 37. The zone in which the lateral buds arise lies about midway between the neck of the median polypide and the tips of its tentacles at this stage. The place of appearance in this zone is approximately 90° to the right or left of the neck of the polypide of the median individual. In one case measured, however, that shown in Figure 20 (Plate II.), the centres of the two lateral buds seemed to be unequally distant from the neck of the polypide, and each over 90° from it (approximately 100° and 110° respectively. (Compare page 3.)

A cross section of the branch through the region in which the lateral bud is arising shows that the condition of the body wall at the bud is quite different from that of the rest of its extent. Figure 19 represents a longitudinal section of a portion of the body wall passing through the non-budding region. The wall seems to consist of one layer only of cells, and a fine, non-stainable cuticula. This layer of cells is the ectoderm, for it can be traced directly into the outer layer of the tip. The mesodermal layer is not represented in the region from which the figure was drawn, but I believe it is not entirely absent from this part of the individual, for occasionally extremely flattened cells, spindle-shaped in section, may be seen lying inside of the ectodermal layer, quite sharply marked off from it by a distinct line. Further evidence of the existence of two layers is found in the fact that one occasionally sees in the flattened body wall two nuclei lying together, one nearer the cœlom than the other. The cells of the ectoderm are seen to be very much flattened (average 2.5 μ), and their nuclei are widely separated (35 μ). The nuclei are oval, and rather smaller than those near the tip. They possess a single, rather large nucleolus, which does not stain intensely. The cell protoplasm stains very little. The cuticula is about 0.5 μ thick.

If we study the body wall in the budding region, when the latter is first indicated on the surface by a marked protrusion of the outline of the zoœcium (Plate II. Fig. 15), we find that this protrusion is due to an elongation of cells. There are about twenty-two cells in this section, which are more or less thickened. Since the section figured passes through the centre of the circular thickening, and is about one sixteenth the diameter of the circle in thickness, it follows that there are over 250 cells of the ectoderm which have already at this stage become somewhat enlarged previous to evagination. The highest of these cells are the central ones, of which the largest is 22 μ high. The largest nuclei are 4 μ by 6.3 μ, which approximates the size of those in the gemmiparous region (page 6). They are placed nearer the cœlomic epithelium than the exterior, are nearly spherical, and each possesses one large nucleolus and a quite apparent network with deeply stainable nodal points. The cell body is stained as a whole rather deeply by Ehrlich's hæmatoxylin, but particularly around the nuclei. The outer parts of the central cells, however, are stained very little, and the deep ends of some of the lateral cuboid cells not at all. The network of plasma contains only fine granules, and these seem to lie in rows parallel to the long axis of the cell. The structure of the outer-layer cells, at a somewhat earlier stage, is shown in Figure 18, under a higher magnification. The network is very apparent in these large spherical nuclei, and the plasma of the cell is seen to contain coarse granules, which lie near the nuclei and stain deeply.

While the cuticula of Figure 18 is seen to be that of the normal body wall in this region, that shown in Figures 15 and 16 appears under the microscope after staining in hæmatoxylin to be of two distinct kinds: (1) that outside of the central region, which is highly refractive and not at all stained; and (2) that which lies immediately over the central elongated cells of the bud, which is also highly refractive but stains deeply. In fact, the central cuticula resembles in every way that already described for the tip of the branch, and shown in Plate I. Fig. 6. Moreover, it has other points of resemblance to the latter. It does not stain at all in alum cochineal; the outer boundary of the branch is often uneven at this place (Fig. 16); and particles of dirt are often found adhering to it, while the rest of the cuticula is comparatively free. The difference in staining properties of the central and lateral cuticulas indicates that the former undergoes with age a change in its chemical properties; the irregular outer boundary and the adhesion of dirt particles seem to indicate that the newly formed cuticula is viscid. The mesoderm of the stage of Figure 15 consists of a single loose layer of subspherical cells of the two kinds already noticed, reticulated and non-reticulated. The series of Figures 18, 15, and 16 shows the behavior of columnar cells in the formation of a typical outfolding as distinguished from the slipping in of cells to form the polypide (Figs. 3, 4, and 5).

In stages later than that of Figure 16, the tip of the branch becomes further removed from the body wall of the median branch. The cells at the tip always retain their elongated columnar condition. A polypide is soon formed on the upper part of the body wall immediately behind the tip, exactly as in the case of the median branch. A septum is very early formed, cutting off the lateral from the median individual, and the lateral secondary branch becomes the median primary one of new individuals (Plate VI. Fig. 58).

We have already traced out the origin of the polypide of the median branch from the mass of cuboidal cells near the tip; it remains to determine whether the cells which give rise to the lateral branch can be traced directly back to the cuboidal cells of the tip, or whether they have arisen from the flattened epithelium of the general body wall and secondarily acquired their plump "embryonic" character.

Figure 18 (Plate II.), to the cellular conditions of which I have already referred, shows an early stage of the lateral branch, and Figure 20, *gm. l.*, shows on a smaller scale the different cellular conditions in the body wall in the region of two lateral buds which are yet far from showing external signs of evagination. The cells are cuboid and much higher than those of the adjacent body wall. Have they been so ever since they were derived from the tip, or have they secondarily become so ? I believe that these cells have never been flattened pavement epithelial cells, for the following reason. All ectodermal cells of the body wall near the tip are cuboidal; if these cells have only secondarily acquired this form, they must have passed through a stage in which they were flattened epithelium. Now, if these cells could be distinguished by greater thickness from the cells of the surrounding body wall, at a time at which the latter cells had only just begun to emerge from the cuboidal condition to become differentiated into the pavement epithelium of the body wall, it would follow that, even though they had secondarily increased in size as a result of an impulse preparatory to evagination, and even though they would have been at a stage only a very little earlier indistinguishable from the other cells of the body wall, yet they would never have passed in this case through a flattened condition, because at a stage only a very little earlier the whole body wall was composed of cuboid cells.

The conditions which I have set as the criterion of our problem are fairly realized in Figure 17, which represents a portion of the body wall of a median branch which extends from the gemmiparous region above to the thickened body wall of the nascent lateral bud below (*gm. l.*). It will be seen, by a comparison of the body wall of this region with that shown in Figure 19, which is taken from the same individual farther from the tip, that even the most differentiated part of the body wall of Figure 17 is in a relatively indifferent condition as compared with the pavement epithelium of the ectoderm of Figure 19, in which the mesoderm, indeed, has become so thin and insignificant as scarcely to be visible. We may, therefore, maintain that the ectodermic cells of the body wall have only just begun to lose their cuboidal condition to become pavement epithelium, and therefore conclude, in accordance with the argument just presented, that the cells of the lateral bud (*gm. l.*) have never passed through a stage in which they were flattened epithelium. It is evident, also, that the *Anlage* of the second lateral bud is also derived from near the tip, because, as in Figure 20, we find two lateral regions of cuboidal cells.

5. Development of the Body Wall.

It is, of course, almost impossible to gain direct evidence upon the place of origin and method of development of the body wall, and one is therefore forced to the collection and weighing of circumstantial evidence. Braem ('90, pp. 127, 128, 131) believes that the body wall (the cystid, in Nitsche's sense) has a double origin in Paludicella: "Ein Theil des Cystids zwar vor dem Polypid, ein anderer aber erst später angelegt und zwar aus der polypoiden Knospe selbst entwickelt wird." The part developed from the bud of the polypide is the elliptical region of the body wall, whose main axis lies in the sagittal plane and which has the neck of the polypide at the distal focus and the attached ends of the retractor muscles and the parietovaginal (or pyramidal) muscles lying in the proximal circumference, — the greatest part of the ellipse thus lying oral of the atrial opening. The evidence for this conclusion Braem finds in the following facts, which my own observations confirm: "The great retractor first appears in the angle between the oral part of the polypide bud and the cystid wall [cf. Figs. 23, 24, *cl. mu. ret.*]; then its cells gradually become elongated, and as its point of origin retreats farther and farther from the polypide, it finally appears as a bundle which joins a point lying between the mouth of the polypide [neck of the polypide] and the inferior septum with the pharynx, and, as I believe, also with the cardial part of the stomach" (p. 125). Compare the muscles at the left end of Plate I. Fig. 8. Further on he says: "Die Parietovaginalmuskeln [pyramidal muscles] erscheinen an der Knospe zuerst in Form zweier seitlichen Leisten, in welchen die einzelnen jugendlichen Fasern senkrecht zur Längsaxe verlaufen. Indem sich alsdann lateral von der Knospe das Cystid durch Neubildungen erweitert, werden die Fasern verlängert und die beiden Bündel treten in Flügelform deutlicher zur Rechten und Linken der Mündung hervor. Ihr Ursprung an der Cystidwand rückt nun von der Mündung immer weiter ab und gelangt schliesslich auf die gegenüberliegende Seite, wo er anal und lateral seinen definitiven Platz findet." Compare Plate I. Figs. 7–9, *mu. pyr.*, and Plate VI. Fig. 63, *mu. pyr.* From these observations Braem ('90, pp. 127, 128) concludes: "So scheint es sicher, dass auch hier ein grosser Theil des definitiven Cystids, das ja zum anderen Theil schon vor der polypiden Knospenanlage entwickelt war, aus dem Material dieser letzteren hervorgeht. Das folgt namentlich aus der Art und Weise, wie sich die Muskeln bilden. . . . Auch hier würde, wie bei den Phylactolæmen, oral vor der Knospe nach dem Retractor hin, ein grösseres Gebiet der Leibeswand der Knospenanlage entstammen, als seitwärts und hinten."

An analysis of the facts has led me to conclusions differing somewhat from those of Braem; namely, that all or nearly all of the cells of the body wall (cystid) are derived from the tip of the branch or from the immediate descendants of cells so derived. The number of cells contributed to the formation of the body wall by the neck of the polypide is much smaller than Braem has suggested, and probably insignificant in amount. The retreat of the points of origin of the retractor and parietovaginal (pyramidal) muscles may be in part accounted for by the normal growth in area of the body wall, and in part by the actual movement of the point of origin with reference to the cells of the body wall. These conclusions rest upon the following circumstantial evidence.

Owing to the small number of cells in the body wall at the tip, and the comparatively slow growth of the cystid, karyokinetic figures are much less frequent than in the polypide. Quite a long search has therefore not afforded cases enough to enable me to draw any perfectly satisfactory conclusions as to just where, and where only, growth was taking place. I have, however, seen nuclear division occurring in the elongated cells of the extreme tip, rather more abundantly in the cuboidal cells between the extreme tip and the gemmiparous zone, and most abundantly in the gemmiparous zone, but here evidently having to do with the origin of the polypide, muscle cells, etc. Proximal to the gemmiparous zone, I have noted few cases of nuclear division excepting about the neck of the polypide. It seems probable that the cells of the tip of the branch are not to be regarded as forming a differentiated organ whose elements rarely divide, but as quite capable of adding new cells to the body wall. On the other hand, there is by no means a *Scheitel* in the botanical sense, but the cells added to the body wall continue for a time to divide vigorously, and finally give rise to the polypide, to the *Anlage* of the lateral branches, and to the body wall. The cells belonging to the proper cystid then cease to divide rapidly.

I have already shown how the cells of the tip secrete a cuticula, which becomes gradually replaced by a second cuticula secreted beneath it as the body wall attains its adult dimensions. It appears as though the first cuticula were secreted by the cells of the tip *only*. This being so, since the area of the body wall increases, this first cuticula must either stretch to cover the enlarged area, or else it will fail to cover it and appear as isolated patches upon the body wall, and these isolated patches will become more and more widely separated as the area of the body wall increases. This latter condition seems to be the one realized in this case. The presence of the old cuticula is easy to demonstrate, since it stains deeply in hæmatoxylin ; and it may be easily distinguished from that formed later, for with the same reagent this stains not at all. Figures 6, 11, 12, and 13 show different appearances of the cuticula at different parts of the body wall. At the extreme tip (Fig. 6) there is a continuous deeply stained band of cuticula. In Figure 11 it no longer appears quite homogeneous, but is darker at some places than at others. The ectoderm is here composed of cuboidal cells. At a later stage of development the ectodermal cells have become very much flattened. A thin, unstainable, more deeply lying cuticula has already begun to form, and the outer deeply stainable cuticula is seen to be broken up into bits. Figure 13 is from the adult body wall. The ectoderm is flattened. The inner cuticula has attained a great thickness, and the outer cuticula is represented by only a few deeply staining patches. One attains a similar result by studying the surface of a stained individual. Figure 10 shows the condition of the outer cuticula at intervals along the same branch from the gemmiparous region *a* to a nearly adult region, *d*. The bits of cuticula become more and more widely separated and smaller, as I have already described in detail on page 7. Here, then, we have not merely an interesting case of replacement of one cuticula by another to meet the needs of the enlarged body wall by a method which has no parallel, so far as I know, in any other group of animals, but for the specific purposes of our problem *a criterion of growth of the body wall* quite as satisfactory as karyokinesis, and much easier of application.

Let us apply this criterion in our attempt to answer the question, Is that portion of the body wall lying between the neck of the polypide and the points of origin of the pyramidal muscles (Plate VI. Fig. 63, *b–a*, *b–c*) derived wholly from the neck, or is it merely the result of interstitial growth of that part of the original cystid which was preformed in the neck region? If the first condition is true, we should expect to find no indications of the outer cuticula secreted by the tip of the branch; if the second, we should expect to find the outer cuticula broken into bits, and underlaid by the inner lately formed cuticula. Figure 63 shows clearly the deeply stained outer cuticula here separated into bits, and, to my mind, thereby proves that this part of the cystid has had an origin similar to that of the rest of the body wall. Moreover, a comparison of the portion of the section figured with the remainder (and this comparison has been made on many sections from several individuals) shows that the parts of the cuticula about the neck are indeed rather smaller and farther removed from each other than at the opposite side of the branch; but the difference in this respect is not very marked, and may well only signify that there is a more rapid growth of the body wall in the vicinity of the neck of the polypide than at the opposite side.

But how then do the points of origin of the pyramidal muscles come gradually to move away from the neck of the polypide at which they arose, in order finally to lie so that the muscle fibres are nearly parallel? If the points of origin remain fixed with reference to the surrounding cells, they can hardly come to lie *absolutely* closer together, but only *relatively* so by growth of the body wall between these points and the neck. If, however, we find that in older individuals the points of origin are not only relatively but absolutely closer together, we are driven to the conclusion that these points move relatively to the surrounding cells. To decide whether the points of origin come to lie closer together behind the neck *absolutely* or only *relatively*, I measured cross sections of four individuals through the region of the neck in which the muscle fibres showed evident differences of length, and therefore of age. I may preface a table of these measurements with the statement that the muscles first appear plainly differentiated at a stage when the polypide is well formed (Fig. 7, *mu. pyr.*), and that the growth of the body wall in circumference is not very considerable after this time. The numbers indicate measurements in micra: —

	No. 1.	No. 2.	No. 3.	No. 4.
Distance on periphery between origins of muscles, atrial side	150	154	187	260
Distance on periphery between origins of muscles, abatrial side	297	286	264	220
Total length of periphery	447	440	451	480

The distance on the "atrial side" signifies the distance measured over *a*, *b*, *c*, Figure 63 (Plate VI.). The length of the remainder of the section is the distance on the "abatrial side."

From these measurements it appears that the "origins" of the pyramidal muscles approach each other absolutely, — a condition which Braem's hypothesis cannot explain, and which can be reasonably interpreted, it seems to me, only by assuming, however unique and difficult of conception such a condition may be, that the points of origin move relatively to the surrounding cells of the body wall. (Compare also the movement of parietal muscles referred to on page 29.[1])

It is not necessary to assume that the increase in extent of the body wall after the polypide is first formed is due to the addition of cells from the neck. The change in form of the ectodermic cells from a columnar to a pavement epithelium must alone cause a great increase in the extent of that layer. Some measurements that I have made seem to me to prove that the area of the body wall does increase greatly, even outside the region whose growth Braem attributed to the addition of cells from the neck of the polypide. Thus, in one case, the distance from the distal end of the polypide bud, which becomes the neck of the adult, to the point of origin of the young retractor muscle was 0.17 mm.; from the same point to the septum separating the young individual from the next older was 0.27 mm. In the next older individual, from the neck to the origin of the retractor muscle was 0.72 mm.; from the neck to the septum was 2.0 mm. Thus assuming that the older individual passed through a stage exactly equivalent to that in which we find the younger, the distance from the neck to the origin of the retractors has increased 0.55 mm., and from the origin of the retractors to the septum 1.18 mm. The first distance is that in which Braem has assumed the body wall to grow by additions from the neck of the polypide, and this assumption was apparently made to account for the increase in extent of this region; but the area between the origin of the retractors and the septum, which is outside the region to which additions such as Braem contemplates could have been made, has grown in this case very considerably more in extent. This case is not a typical one, however, for we rarely find the distance from the origin of the retractor to the septum to be so great. In general, from observation of a number of cases, I should say that in the adult the distance between the neck of the polypide and the origin of the retractors, is to the distance between the latter and the septum about as 5 : 4, and that therefore the growth of the first region is slightly greater than that of the second. From the fact, however, that the cells around the neck of the polypide for a long time retain a somewhat embryonic character, and may quite frequently be seen in division, this was to have been expected. The conclusion which I draw from this last series of conditions is, then, that it is unnecessary to suppose the addition of cells from the neck of the polypide to account for the fact that the origin of the retractors is carried backward from the polypide. Normal growth of the body wall, such as occurs elsewhere, is quite sufficient to account for it.

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[1] Professor Mark has called my attention to a discussion of the movement of the fixation-point of a muscle in Mollusks by Tullberg ('82, pp. 26, 27, 44). This author says that he has undertaken no special investigation of the method of migration, but concludes that this motion must result from the absorption of the inner muscle fibres as new ones are formed on the outside. I do not find any evidence of such a process in Paludicella.

To recapitulate. That portion of the cystid lying in the vicinity of the neck can hardly be derived from the neck alone, for the cells still show adhering to them the cuticula which they derived from the tip of the branch. It is not necessary, in order to account for the movement of the origins of the muscles away from the neck, to suppose that the circumcervical region is derived in that way; for (1) the origins of the pyramidal muscles actively migrate away from the neck to a certain extent, and (2) the normal growth of the body wall is sufficient to account for the carrying backward of the origin of the retractors.

From the facts already gained it seems clear that the ectocyst (cuticula) is first formed at the tip, and then, to meet the wants of the growing colony, this is replaced later by a cuticula of different chemical composition, which becomes thicker as the body wall grows older. At a late stage we find a separation of the thick cuticula itself into two layers, of which the outer one is much the more highly refractive.[1] (Plate II. Fig. 13; Plate III. Figs. 26, 29.)

6. Development of the Polypide.

We have already (pages 8, 9, Figs. 5, 14, 37) seen how the foundations of the polypide are laid by the ingression of cells of the outer layer of the body wall pushing before them the mesoderm, and how, finally, those cells arrange themselves in a boat-shaped mass to form the inner layer of the bud (Plate III. Fig. 21), which possesses no actual cavity, and is constantly separated from the external world by the ectoderm which remains behind to form the neck of the polypide. Even when a cavity is formed later, it does not communicate with the exterior until the permanent atrial opening has arisen. The earliest differentiation in the bud is, as mentioned by Allmann ('56, p. 36), the formation of a cavity which is to become that of the atrium. This cavity is first formed at an early stage as an extremely slight fissure in the midst of the inner layer. Figure 22 shows a longitudinal section of this stage. Cell division is taking place throughout the whole mass, but especially at the neck of the polypide, *cer. pyd.* The position of the cavity is represented by the central non-nucleated space, and this gives rise, as the later history of development shows, to the atrium and the pharynx.

Figure 23 represents a stage which is doubtless of short duration, for I have found it only twice. The bud is much more developed at the anal end than in the last stage, and there is a second cavity below the atrium, from which it is separated by a line of nuclei. This is plainly an early stage in the formation of the *alimentary tract*, which thus first appears at the anal side of the bud, as in Phylactolæmata, and is progressively formed towards the oral end. An appearance similar to the one figured would be given by a slightly oblique section of a later stage; but this section is strictly sagittal, and no trace of the lumen appears in adjacent sections. I have found a similar condition in a series of longitudinal sections at right angles to the sagittal plane of the bud (Plate IV. Figs. 39 and 40). Figure 39 shows that the atrio-pharyngeal cavity is first developed at the anal end, and in Figure 40, which is three sections (about 15 μ) below Figure 39, the anal end only of the alimentary tract is formed. It is worthy of notice that the cells of the mesodermic layer of the bud are often greatly vacuolated at this stage, as in Figures 39 and 40, *vac.* Braem ('90, p. 126) says of this stage: "Die der Resorption dienenden Darmabschnitte, Magen und Enddarm, werden gemeinsam angelegt, indem auf jeder Seite der Knospe eine Längsfalte die Wandungen nach innen und gegen einander zu einbiegt, worauf die benachbarten Theile des inneren Blattes verschmelzen und so durch eine Art Abschnürung das primäre Knospenlumen in den vorderen Atrialraum und die hintere Darmhöhle getrennt wird." While I thoroughly agree with this statement, the additional fact of the formation of the tract *progressing from the anal towards the oral end* is interesting, in that it shows that the process of formation of the organ in Paludicella is fundamentally similar to, although differing slightly in detail from, that of the Phylactolæmata. Figure 24 shows in sagittal section a still later stage in the development of the alimentary tract. A cross section of this stage is seen in Figure 30 (Plate IV.), in which the separation of atrial and gastric cavities is demonstrated. The inner layer of the bud is here seen to be separated from the ectoderm by a distinct line, and, to a certain extent, even by the mesoderm. The distal (oral) part of the cavity of the alimentary tract next becomes considerably enlarged to form the stomach (Fig. 25). The outer layer of the bud, *ms'drm.*, penetrates between the stomach and the atrium, and a depression is formed at the bottom of the atrial chamber which will give rise to the œsophagus. Even at this stage the œsophagus is not in communication with the stomach, but their cavities are separated by two layers of cells of the inner layer of the bud. These two layers become those of the cardiac valve (Plate IV. Fig. 36, *vlv. cr.*). By a further comparison of Figures 25 and 36 it will be noticed that, whereas in the earlier stage, as in Endoprocta, there is no cæcum to the alimentary tract, in the later stage the cœcum has already begun to form, as in Phylactolæmata, by an outpocketing of nearly the whole of the lower wall of the stomach. (Compare also Plate I. Figs. 7, 8, and 9.)

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[1] Such a two-layered condition of the cuticula was long ago described by Reichert ('70, pp. 265, 266) for Zoöbotryon. He distinguished "eine *äussere, festere,* stärker lichtbrechende und sprödere Schicht und die *innere weichere.*" Realizing that the "ectocyst" or cuticula undergoes many changes in form, — formation of lateral buds, of septæ or communication plates, and increase in size of the stolon, — he suggested, without having observed the process, that probably during these changes the more rigid outer layer disappeared and was replaced by the inner softer one.

Very soon after the establishment of the alimentary tract, and between the stages shown in Figures 24 and 25 in sagittal section, there begin to appear organs which have a very considerable phylogenetic significance; namely, the lophophoric ridges, ring canal, and tentacles.

The *lophophoric ridge* is a fold which surrounds the mouth, and from which at intervals tentacles arise. The ridge, however, arises before the tentacles. The general position of the ridge, as well as its method of origin, may be learned from an inspection of a series of sections of the age of those shown in Figures 31–34. In a section lying near the oral end of the bud (Fig. 33), one finds two spaces, — a lower, which is that of the stomach, and an upper, the œsophagus and atrium. This upper space is broader above than below, and the cell layer which lines it is thick below, but above, or nearer to the body wall of the budding individual, it is thinner. The transition from one condition to the other is quite abrupt, and is marked by a salient curve (*loph.*). In a section near the anal end of the bud (Fig. 31), it will be seen that here too the inner layer is thick below and thin above. The characters mentioned are still more strikingly shown in the median section, Figure 32. That the differences in thickness of different parts of the inner layer are recently acquired modifications of an earlier simpler condition is indicated by comparing Figure 32 with Figure 30, which is from a younger bud. The series of points (*loph.*) of transition from thick to thin epithelium forms on the reconstructed polypide a curved line, convex above. This line is the ridge of the young lophophore (compare Fig. 25, *loph.*). I have said that the lophophoric ridge arises before the tentacles. The evidence for this assertion is found in a series like that referred to above, where, although the ridge exists along the entire side of the atrium, one finds nascent tentacles in the middle region only (Figure 32, left hand).

As Figure 25, of a later stage than Figures 31–33, shows, the lophophore curves downwards rapidly at the anal end, so that it here lies at right angles to the axis of the rectum, but does not extend at all beyond the anus. Orally, there is in the median plane only the slightest trace of the lophophoric ridge. By the formation of this ridge in the wall on each side of the atrial chamber, the original atrio-pharyngeal cavity has become separated into two regions. The space lying within or below the ridge forms the pharynx and the intertentacular space; that lying without and above, the atrium of the adult. (Plate III. Fig. 25; Plate IV. Fig. 32, *atr.*) Since the lophophore curves rapidly downward to the anus and does not extend behind it, the act of cutting off the lower part of the atrio-pharyngeal cavity from the upper (atrium proper) does not continue behind the anus, which therefore opens directly into a part of the atrium. This part has the form of a compressed funnel, and is bounded behind and laterally by the kamptoderm, and orally by the hinder ends of the lophophoric ridges, and also, since the latter do not meet in the median plane, by the pharyngeal cavity. Thus it has come about that the anus, which at first opened into the common atrio-pharyngeal cavity of the bud, has now, in the separation of the two regions, come to lie near their point of division posteriorly, but to open distinctly into the atrial cavity. The more pronounced separation of the part of the atrial cavity into which the anus directly opens from the remainder of the atrium takes place much later, and will be described further on.

In Figure 33, the *ring canal* (*can. crc.*) is seen to be already formed. At this stage it is found on one side only, the left, if one looks at the polypide from the tip of the branch. It occurs in only four sections (each 5 μ thick), being found on the next section behind Figure 33, and on two sections nearer the oral end. At its oral extremity, it terminates blindly as a thickening of the outer layer of the bud; at its anal end, one sees cells of the outer layer extending out partly over the canal, but failing to enclose it; in the next section the mesoderm is undisturbed. In similar sections of an older polypide (corresponding in age approximately to Plate IV. Fig. 35), the canal is found on both sides, and near to the oral end, but at about the middle of the series (cf. Fig. 35) it is found to open again into the body cavity. I therefore conclude that the ring canal makes its first appearance at the base of the lophophore in a region just oral of the middle of the polypide. Exactly how it arises, whether by a growing together of the lips of a shallow furrow formed from the mesodermal layer, or by the formation of a pocket, which, elongating, penetrates between the inner and outer layers of the polypide at the base of the nascent lophophore, I have not been able to determine. Two facts induce me to believe that the later formation of the canal oralwards results from the penetration of a sac-like mass of mesodermal cells between the two layers of the polypide at the base of the nascent lophophore. One usually finds, (1) as in Figure 33, *can. crc.*, a double mesodermal wall between the lumen of the canal and the cœlom, and one layer between the former and the inner layer of the bud; and (2) at the oral blind end of the ring canal a number of loose cells (occasionally dividing) representing the blind end of the pocket and lying between the inner and outer layers, both of which are intact.

Braem ('90, p. 50) describes the formation of the ring canal in Phylactolæmata as taking place in the manner just suggested for Paludicella. His studies were made, he says, preferably on statoblast animals. Nitsche ('75, p. 358) concluded that in Phylactolæmata the ring canal was first a furrow, whose lips fused, and my own study ('90, p. 129) has led me to the same conclusion. Since reading Braem's account I have looked over some of my own sections of Cristatella again. Certainly the process is not so clear in the buds of the adult colony as in the statoblast embryo which Braem figures. Nevertheless the series of sections ('90, Plate IV. Figs. 33–38) given as evidence of my statement still seem to me capable only of the conclusion I drew from them. Perhaps the processes may be different in detail in the two cases; certainly the two explanations are not fundamentally dissimilar.

The ring canal being established in the oral part of the polypide, it grows forward, as I have said, and, secondarily, the canals of both sides meet in the median oral line and their lumina become confluent (Plate VI. Fig. 52, *can. crc.*). From what has already been said, it is clear that the lateral parts of the ring canal are not now continuous with each other behind. They become so only after the formation of the tentacles.

The *tentacles* arise upon the lophophoric ridge at a stage a little later than that represented in Plate IV. Figure 32. At the stage represented by Figure 35, however, the tentacles have begun to form, as indicated by the fact that in the series from which this figure was taken the fold into the upper part of the atrium appears now deep, now shallow, according as the section passes through the length of a young tentacle, or only through the lophophoric ridge between the tentacles. The position of the section (Fig. 35) is about the middle of the series, corresponding to Figure 32.

By a comparison of Figure 35 with Figure 32 in respect to the tentacles, it will be apparent, first of all, that the lophophoric ridge itself has been heightened and that this heightening has been effected, not by a deepening of the fold existing in Figure 32, the lips of the fold remaining quiescent, but by a movement downwards of the outer lip (*) of the groove which is to form the ring canal. The movement is of course accompanied by an increase in the length of the kamptoderm, *kmp. drm.* This growth of the lophophoric ridge naturally does not result in making the tentacles project farther above the ridge. Their elongation must take place quite independently of the former's. The lophophoric ridges have now become elongated folds lying upon the right and left of the polypide, which at this stage has a very compressed appearance (Plate IV. Fig. 41). The folds occupy the position of the ridges, and therefore do not lie throughout their whole extent in one plane, but oralwards are nearly parallel to the body wall (Plate III. Fig. 25), analwards trend nearly at right angles to it. It results from this fact, that one cannot see the anal tentacles when looking at the polypide from the side of the body wall to which it is attached. Figure 41 (Plate IV.) shows also that no tentacles have yet made their appearance at the oral ends of the two lophophoric ridges.[1] The tentacles are here seen to be arising in two long rows, and so that those of one row are placed opposite the intertentacular spaces of the other. There are six tentacles in each row. The rows are not continuous with each other oralwards or analwards.

The separation of the atrial and oral cavities, begun by the first formation of the lophophore, is, now that the tentacles have arisen, much more pronounced. Other changes now occur in this region, which produce an extensive modification in the form of the polypide.

One of the first of these changes is the close approximation and finally fusion of the anal extremities of the lophophoric ridges oralward of the anus. A stage in this is shown in Figures 43 and 44 (Plate V.), which are sections in the position of the lines *43, 44,* of Figure 25 (Plate III.), but through a slightly older polypide than that represented by Figure 25. The section shown in Figure 43 passes across the rectum, grazes the outer lip of the ring groove of the anal tentacles, and finally cuts, nearly longitudinally, one of the middle tentacles of the row. The two lophophores are not yet completely fused in front of the rectum. In Figure 44 (compare Plate III. Fig. 25, *44*) this break in the continuity of the lophophore is more prominent.

By the completion of the union of the lophophores in front of the anus, the rectum is quite cut off from communication with the intertacular space. It now opens only into the thin-walled, funnel-shaped depression of the atrial cavity.

Pari passu with this operation the stomach and rectum are being more completely separated from the pharyngeal cavity by the penetration of a double layer of mesoderm between these regions from each side, and a fusion of the corresponding layers of the two sides. Finally, the walls of the stomach and pharynx become separated from each other by a part of the cœlomic cavity, as in Plate IV. Figure 36. This process of separation of the alimentary tract proceeds analwards, and finally the rectum is far removed from the œsophagus.

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[1] Compare Plate IX. Figure 77, which is a superficial view of the young lophophore from Flustrella, in which the process is similar to that in Paludicella, only the down curving of the anal tentacles occurs later than in the latter case.

The anus thus comes to lie farther outside of the anal tentacles. Finally, the ring canal, which is formed progressively farther and farther analwards, follows the fusion of the anal ends of the lophophores, and thus completes the canal behind the œsophagus. (Plate IV. Fig. 36; Plate VI. Fig. 53, *can. crc.*)

The anal part of the ring canal is doubtless not merely a groove, but a tube; but the ring canal is not closed at this, and probably not at any stage throughout its entire extent, for in Plate VI. Figure 52, two sections below Figure 53, an opening is shown to exist on each side (at *can. crc.*), putting the cavities of the ring canals and the cœlom into communication with each other. These openings lie at the sides of and slightly above the ganglion (*gn.*, Fig. 52); a position exactly comparable with that of the openings in the ring canal of Phylactolæmata, which leads from the cœlom into the lophophoric arms on the one hand, and into the circumoral part of the ring canal on the other.

By a comparison of Figure 41 (Plate IV.) with the sections shown in Figures 60–62, it will be seen that the row of tentacles has undergone a change of form: from being laterally compressed, it has become circular. This change of form has not resulted from an increase in the number of the tentacles, for at the stage of Figure 41 there are six tentacles on each side already formed (the sixth not visible), and there are in front of the mouth spaces already reserved for the two additional tentacles. There are also, probably, two nascent tentacles at the anus, although these are little developed, making a total of 16. In Figure 61 there are only 15 tentacles; moreover, the actual diameter of the tentacular corona in the sagittal plane is less than at the earlier stage of Figure 41. This change of form is perfectly normal, all young polypides having tentacles arranged in two parallel rows, and adult polypides having a circular lophophore.

These changes in the form of the tentacular corona are correlated with important changes in the direction of the axes of other organs. These changes may be understood by comparison of Figures 25 and 36, together with the assistance of Figures 7–9, all of which are oriented in the same manner. In Figure 25 the points fixed by the cardiac valve (*vlv. cr.*) and anus (*an.*) lie in a line which is approximately parallel to the body wall. In Figure 36 the line passing through the same points makes an evident, but not very large, angle with the body wall. This line has undergone, then, a slight change of position only. The axis of the anal tentacles lies in both cases nearly parallel to the body wall, and so does the neural wall of the pharynx. The oral tentacles, on the contrary, whose axes in the earlier stage are directed perpendicularly to the body wall, lie in the later stage with their axes parallel to the wall; and the base of the lophophore, which in the earlier stage trended at its oral end parallel, at its anal perpendicular to the body wall, in the later lies throughout its whole extent in one plane perpendicular to the body wall. The axes of the oral tentacles have rotated through an angle of nearly 90° relatively to most of the other organs of the polypide. The cause of this rotation must evidently be sought in unequal growth in different parts of the polypide. A comparison of the length of the kamptoderm on the anal side in Figures 25 and 7 indicates that it has grown more in length than on the oral side. This excessive growth would tend to rotate the line *vlv. cr.* — *an.* to a position perpendicular to the body wall. Since this rotation has not occurred to so great an extent as was to have been expected, we must look for a compensating growth on the oral side of the polypide, between *vlv. cr.* and the neck of the polypide, which shall be nearly equal to the excessive growth of the anal kamptoderm, and which must be *outside* of the oral kamptodem. These conditions of location are fulfilled only by the oral wall of the œsophagus, and it is by change of position and growth of this wall that the extension of the anal kamptoderm is nearly compensated for on the oral side of the polypide. By this growth in the wall of the œsophagus the oral part of the ring canal has been brought to lie over the anal part, the sagittal diameter of the tentacular corona has been reduced, and the compressed lophophore has been transformed into a circular one.

Concerning the number of tentacles, Dumortier et van Beneden ('50, p. 46) observe that in the adult there are ordinarily 16, although individuals with 18 tentacles occur not infrequently, an observation which Kraepelin ('87, pp. 98, 99) confirms. In addition to these numbers, I have found 15 and 17. The growth of the odd tentacle is quite interesting. The sections reproduced in Figures 60–62 (Plate VI.) will serve to illustrate a condition which I have quite frequently found in a polypide with 17 tentacles. In this particular series there are only 15 tentacles. The successive sections abundantly demonstrate that the odd tentacle (*) is anal in position, and that it is younger than any of the others; thus in Figure 61 its tip is cut, in Figure 60 there are only 1½ tentacles visible, and these are found in the two following sections. Since there are six sections which pass through the tentacles, and the odd tentacle is found in only three of these, it follows that it is only about one half as long as the others.

The *nervous system* arises, as in Phylactolæmata, by a depression in the floor of the common atrio-pharyngeal cavity, in the region which later becomes the anal surface of the pharynx. As in Phylactolæmata, we first see a shallow pit (Fig. 25, *gn.*). This appears to become deeper, sinking downward and somewhat toward the cardiac valve (Fig. 78, *gn.*). Finally it becomes constricted off from the wall of the œsophagus, and then appears as a cellular mass closely attached to it and surrounded exteriorly only by mesoderm. (Plate I. Fig. 8; Plate VI. Figs. 52, 53, *gn.*) Even before the closure of the ganglionic pocket is completed, the formation of the circumœsophageal nerve, first described by Kraepelin ('87, pp. 62, 63) in the adult, begins.

Figure 52 (Plate VI.) shows a transverse section of a young polypide in which the ganglion is solid, and not provided with a large cavity as in Phylactolæmata. There is a small cavity in the upper part of the ganglion, and this is not yet wholly closed from the œsophagus. The ganglion is continuous with a pair of hornlike processes (*n.*) which partly enclose the œsophagus, and at a later stage do so wholly (Plate IV. Fig. 36, *n'*.) The cells of these horns are found dividing in unusual abundance. The horns lie next to the digestive epithelium, and between it and the mesodermal lining of the ring canal. From the method of growth, and from the sharp line of separation between the tips of the horns and the surrounding tissue, there can be little doubt that the circumœsophageal nerve of Paludicella, like the lophophoric nerves of Phylactolæmata, arises as an outgrowth of the brain.

Serial sections show that the ganglion suddenly diminishes in size immediately below the point at which the circumoral nerves arise, but one can trace a layer of cells continuous with the brain downwards for ten or fifteen micra farther, to near the cardiac valve. At this point one can still see nuclei of a third layer lying between the digestive epithelium of the valve and the mesoderm. It seems to me, therefore, that this may be regarded as a gastric nerve, which seems to originate by a single root and later to give rise to two nerves, one of which lies on either side of the cardiac valve.

7. Origin of the Muscles.

a. Retractor. — After its first formation the bud becomes elongated in the direction of the axis of the branch. The derivation of this elongated stage from the much shorter earlier one might be effected in one of two ways: either, first, by the ingression of cells from the ectoderm at points successively more and more remote from the point of primary invagination, the additions to the length of the bud being made by a continuation backwards of that process by which the first foundations were laid; or secondly, by cell proliferation at the point of first invagination pushing the oral end of the buds farther and farther from the neck of the polypide.

I think there can be little doubt that the second is the method by which the bud becomes elongated; and for the following reasons. (1) The oral end of the bud, on the supposition of continued invagination of the body wall, should become very gradually of less diameter, and transverse sections at that end should exhibit the ingression (potential invagination) of cells which were observed in the earliest stage; but as a matter of fact the oral end is abrupt (Plate III. Fig. 22, 23, *Or.*), and no stages of ingression are to be found there. (2) On the first assumption, the inner layer of the bud should be at all points in equally close relation to the ectoderm of the body wall; on the second, the inner layer should be closely connected with the ectoderm at the neck of the polypide (Plate III. Fig. 22, *cev. pyd.*), but elsewhere it should be sharply separated from it. As a matter of fact, a sharp line can be distinguished, in a sagittal section, separating the inner layer of the bud from the overlying ectoderm at all points except at the neck (anal part) of the polypide (Plate III. Figs. 22–25). Moreover, cross sections of the anal part of the bud show the inner layer passing directly into the ectoderm, and oralward the outer layer of the bud tends to penetrate more and more between the ectoderm and the inner layer. Therefore I conclude that the inner layer of the bud is constantly augmented by cell proliferation in its mass, and especially at the neck of the polypide, and this explanation also accounts for the active cell proliferation observed at the neck in Plate III. Figure 22, *cev. pyd.*

Since the polypide later becomes attached to the body wall by the comparatively narrow "neck" only (Figs. 7, 9, *cev. pyd.*), a separation of the oral part from the body wall has to take place. This process begins at the oral end. In its earliest stages it is indicated by the sharp separation of the inner bud-layer from the overlying ectoderm, and the partial penetration of the mesoderm on each side into the space between these two layers (Plate IV. Fig. 30, *ms'drm.*). At a later stage the mesoderm may be seen as a single cell layer lying between the ectoderm and the inner layer of the bud midway between the oral and anal ends (Plate IV. Fig. 32, *ms'drm.*), and as a double cell layer at the oral end of the bud (Fig. 34, *ms'drm.*). It is from these cells at the oral end of the bud that the retractor muscles are to arise (Plate III. Figs. 23–25, *cl. mu. ret.*). As the oral end of the kamptoderm and œsophagus to which their inner ends are attached moves away from the ectoderm, and as the area of the latter itself increases, the two ends of the cells move farther and farther apart, and the young muscle cells become drawn out into spindle-shaped muscle fibres. (Plate III. Fig. 25, *cl. mu. ret.*; Plate IV. Fig. 36, *mu. ret.*) The retractor thus arises unpaired and remains so at its origin, but nearer its insertion in the ring canal and œsophagus one can distinguish a division into right and left masses. The adult muscle fibres consist of two parts at least, the inner contractile portion and an outer less modified protoplasmic portion, which can be traced over the whole of the first part, but is most evident around the nucleus, where it has a granular appearance.

b. Pyramidalis. — At about the stage of Figure 25 (Plate III.) one finds, on cross sections of the branch which pass through the neck of the polypide, that the mesoderm of the body wall on each side of the neck is greatly thickened, and that its closely packed cells, which lie three or four deep, have become somewhat elongated. Cell division is quite common in the ectoderm of this region, and by it the area of the circumcervical region is increased and the two ends of the muscle fibres are carried farther apart, one end remaining attached to the neck of the polypide and the other moving towards the abatrial surface. I have given reasons above (page 16) for believing that the abatrial ends of the muscles are not carried towards the abatrial side passively, and solely by the growth of the body wall, but that the ends move relatively to the cells of the body wall. A somewhat late stage in the development of the pyramidalis is shown in Figure 63 (Plate VI.). Nearly the whole of the mesoderm of the body wall has here been transformed into muscle cells. The insertion of the muscles is in the mesoderm of the neck of the polypide. (Plate VI. Fig. 63 ; Plate V. Fig. 45.)

c. Parietal muscles first make their appearance at about the stage of the terminal individual of Plate II. Figure 14, immediately below the bud and to the right and left, i. e. so that the muscles, which usually arise paired, have their long axes parallel to the sagittal plane and perpendicular to the long axis of the branch. They arise from cells of the mesoderm, most of which in this region are filled with vacuoles, and often project into the cœlom. But in my opinion the muscle cells do not themselves arise from such vacuolated cells, for at even an earlier stage (corresponding to Figure 21, Plate III.) one can distinguish thickened patches of elongated cells in the mesoderm which are undoubtedly the young muscle cells; but they do not show the slightest traces of being vacuolated, and in fact are sharply distinguished from the adjacent cells by their uniformly granular appearance and their deeper coloration.

Braem ('90, pp. 124, 125) has already stated that the parietal muscles arise in pairs, and come to traverse the cœlom, not remaining in the body wall. The truth of this statement I can confirm in the case of the parietal muscles first formed, which lie near the future septum. Plate V. Fig. 42 shows the origin of the muscle fibres on both sides of the branch. They have already migrated into the cœlom. As Braem plainly states, the component parts of this pair of muscles, developed from the mesoderm, migrate towards each other and finally fuse into one unpaired mass, as we see in Plate III. Figure 26. It is perfectly evident, in this case at least, that both ends of two muscles originating far apart migrate in some manner towards each other so that the corresponding ends come to lie close together. Such a migration cannot be accounted for merely by growth of the body wall. The ends of the muscle fibres must move relatively to the body wall.

When the muscles have reached their permanent positions in a diameter of the branch, we find their ends attached to the cuticula. As the muscle fibres stain deeply in hæmatoxylin, they can be distinctly traced through the vacuolated and poorly stained cells of the body wall (Plate III. Fig. 26). Figure 29 shows a bit of the wall mechanically separated from the cuticula, the end of the muscle fibre remaining in place. Fine lines can be distinguished in the contractile, deeply staining portion of the fibre. The surface by which attachment is effected appears very slightly crenulated on longitudinal sections of the muscle fibre. I could not distinguish any structural peculiarity on the part of the cuticula to which the muscle was attached, — nothing to indicate how attachment is effected.

Freese ('88, pp. 15, 22, Fig. 11) has described a similar method of attachment of the muscles to the cuticula for Membranipora.[1]

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[1] My friend, Dr. G. H. Parker, tells me that a similar method of attachment of muscle fibres to the cuticula occurs in *Crustacea*. According to Tullberg ('82, pp. 27, 44, 45), the adductor muscle fibres are in Mollusks attached to the cells of the ectoderm. The same condition as in Mollusks seems to exist in Annelids (Eisig, '87, pp. 25, 36)

At a later stage smaller bundles of muscles arise successively toward the neck. These muscles are free from the body wall at their middle region. They do not usually pass through the cœlom in a diameter of the branch, however, but rarely subtend as chords an arc of more than 120°. As Braem supposed, such muscles, although arising later than the most proximal pair, originate in a similar manner to them (Plate VI. Fig. 55). The mesoderm is very thin at the region at which they are first seen, and they are quickly discerned by their larger nuclei and prominent cell body. At a later stage they have grown much longer, and become freed from the body wall at their middle part.

As is well known, there are two *funiculi* in Paludicella, called by Allman respectively anterior (nearer the atrial opening) and posterior. The origin of the funiculi of Paludicella was observed by Dumortier et van Beneden as long ago as 1850. They say (p. 54), "La couche muqueuse une fois formée s'étend rapidement dans l'intérieur et touche bientôt par son extrémité inférieure les parois opposées de la loge. Les cellules muqueuses dont le tout est encore composé contractent de l'adhérence dans cet endroit, et c'est ce qui donne naissance au muscle rétracteur de l'estomac [= funiculi]." Allman ('56, p. 36, Plate XI. Figs. 7–9) also describes and figures very clearly and correctly this process, and Braem ('90, p. 127) has recently confirmed their observations.

It is perhaps unnecessary to redescribe the more evident part of this process, the contact of the polypide with the abatrial wall of the branch. The mesoderm of the bud comes into contact with that of the body wall, the cells of each of the two layers become attached to the other, and by the withdrawal of the polypide the attachment persists at two points forming a long drawn out string of tissue. Figures 36^{a} and 38 (Plate IV.) are contributions to a knowledge of the finer details of this process. Apparently the upper funiculus is developed earlier than the lower, as I have always found it longer at about this stage. The lower funiculus at present consists of only the two mesodermal layers of body wall and polypide intimately united. The funiculus itself consists of a cord several cells thick; but I believe these certainly to be derived from the mesoderm only. Very early some of these cells show an appearance of highly refractive and deeply staining fibres, which I interpret as muscular differentiation (Plate IV. Fig. 38, *fun. su.*), so that the funiculi must be regarded as partly muscular in function. As in Phylactolæmata, these fibres lie near the axis of the funiculus. Braem ('90, pp. 66, 67,) has demonstrated that the muscular fibres of the funiculus of Plumatella pass directly into the muscularis of the body wall. It is interesting to find them persisting in the funiculus of Paludicella, beneath the mesodermal covering, although there is apparently no muscularis developed in the body wall of this region.

8. The Formation of the Neck and Atrial Opening.

This is the last act in the history of the polypide that I shall consider. The body wall around the neck of the polypide continues to possess a less differentiated character than the remaining portion for some time after the oral tentacles have undergone their revolution. One still sees the cells of this region dividing, and the body wall is gradually protruded at this point above the general level. (Plate II. Fig. 14, *cev. pyd.*) The neck of the polypide to which the kamptoderm is attached consists, at a somewhat earlier stage than that just referred to, of a disk of greatly elongated columnar cells in the centre of which there is a distinct notch caused by the presence of shorter cells at that point. (Plate VI. Fig. 63 *b.*) At the inner ends of the columnar cells of the neck lies a flat epithelium quite sharply marked off from the latter, but which is nevertheless undoubtedly derived from the same source as the columnar cells and the inner layer of the bud. This flat layer is directly continuous with the inner layer of the kamptoderm. At a later stage, the columnar cells of the ectoderm become elongated still more, and lose their staining capabilities at their outer ends. Still later one sees them arranged in the form of a cup whose cavity is separated from the outside world only by a cuticula which becomes slightly invaginated at this point. The cells are soon found with their long axes perpendicular to the edge of the cavity they line.

There is one point that I have not been able to determine; namely, how the new cuticula, which is certainly formed at the ends of the cells which lie next to the cavity, becomes continuous with the old cuticula of the non-invaginated body wall, as it is in Figure 50 (Plate V.). The presence on the new unstainable cuticula of the remains of the stainable one, whose origin I have already discussed at length, may serve as a guide to the limits of the old cuticula. The new cuticula is being secreted by cells lying deep in the inner end of the neck, and apparently in one rod-like mass. Unfortunately, I lack stages between this figure and Figure 45 (Plate V.), which shows the neck of a nearly or quite adult polypide cut lengthwise. The solid cuticular rod has now become a hollow cylinder, whose inner (deep) edge is embedded in the deep-lying cells of the neck. Moreover, one finds superficial to the cuticula of the general body wall a second cuticular cylinder, which is free at its outer end.

but at its inner end fuses with the surrounding cylinder of cuticula. This inner cylinder, which is probably formed, as Kraepelin ('87, p. 40) suggested, by splitting of the delicate cuticula at the base of the marginal thickening (Randwulst), has been compared by Kraepelin to the "collare setosum" of Ctenostomes. The *Randwulst* itself I believe to be the equivalent of the Diaphragma of Nitsche, as I shall try to show later.

At the deep end of the neck (Fig. 45), the inner layer of the bud is seen to be continuous with the ectoderm. The region of transition may be called the atrial opening, *of. atr.* Surrounding the atrial opening is a fold in the ectoderm, and between the layers of this fold is a thin, non-stainable homogeneous layer, slightly more refractive than the surrounding protoplasm. This membrane extends also a short way into the kamptoderm, and here lies between its two cell layers. Embedded in this homogeneous membrane in the fold, one can distinguish still more highly refractive bodies, *spht.* On account of their form and high refractivity, I believe these to be muscle fibres cut across. The homogeneous membrane has also the same general appearance and relation to the muscularis as the so-called supporting membrane of Nitsche, and it is the only representative of that structure that I have found in Paludicella.

9. Development of the Communication Plate.

In their description of Paludicella, Dumortier et van Beneden ('50, p. 40) say: "Il se compose de plusieurs loges ou cellules placées bout à bout . . . en sorte qu'il n'y a aucune communication entre les différents animaux." Also Allman ('56, pp. 114, 115) refers to the presence of a perfectly formed septum separating the cavities of adjacent "cells." To Kraepelin ('87, p. 38) belongs the credit of having first carefully studied this structure in the adult by means of sections. He came to the conclusion from the appearances which he figures (cf. my Plate V. Fig. 49), that there are small canals passing through the nearly homogeneous central mass, and therefore "dass wir in dem ganzen Apparat eine Vorrichtung zu erblicken haben, durch welche Nährstofflösungen des einen Tieres mittels siebartig wirkender Cautelen in die Körperhöhle des Nachbarindividuums übergeführt werden."

The descriptions of Kraepelin concerning the structure of the "Rosettenplate" are confirmed by my own observations, and seem to justify his conclusions concerning its function. The development of the organ has not, however, been carefully observed heretofore. Korotneff ('74, Plate XII. Figs. 1 and 2) gives figures to show this process, but I have never seen any such circular groove surrounding the branch as he figures. In all cases the two layers of the body wall form a circular fold, in which, however, there is never, even at the earliest stages, a space between the ectodermal layers, nor any infolding of the cuticula as Korotneff ('75, p. 369), according to Hoyer's rather incomplete abstract, maintains (Plate V. Fig. 47). When the circular fold has advanced until only a small pore remains, by which the cavities of the older and younger individuals are kept in communication, the mesodermal cells at the angle of the fold begin to undergo a metamorphosis both in form and histological character. In the first place they become much elongated and extremely attenuated, passing from one surface of the septum to the other, and forming the lips of the pore. In the second place their plasma becomes first deeply stainable, and later, in addition, homogeneous and highly refractive. These metamorphosed cells form what may be called the *teeth* of the plate. They are derived wholly from mesoderm.

The cells in the upper mesodermal layer next increase rapidly in number and size, and the number of teeth is also augmented (Plate V. Fig. 48). The metamorphosis of the cells extends still farther away from the communication pore, and involves the lower mesodermal layer; but, apparently, each cell of the latter is metamorphosed only to a slight depth within its cell wall (Fig. 51), whereas in each of the upper cells the ends which project into the communication pore are modified through and through (Fig. 46). At a later stage (Fig. 49) the metamorphosed part of the cell seems quite sharply cut off from the active part, and the slits between the metamorphosed teeth are considerably reduced. Nevertheless, I believe a transfer of fluids may still occur between them, for even in the adult communication plate one can trace continuous lumina when the cells are by accident torn off from the "teeth" which they have produced. It is important to note that the nuclei are not destroyed in the cell metamorphosis. Some lie above, others below the pore, and become deeply stainable. The ectodermal layers of the communication plate secrete a cuticula between them. This is thinner than that of the body wall, and does not extend, of course, to the centre of the communication plate, but ends in a thickened ring, whose diameter is about one tenth the diameter of the plate, or, absolutely, about 9.4 μ.[1]

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[1] Reichert ('70, p. 267) first carefully described the Rosettenplate of Ctenostomes in Zoöbotryon, and the organ in Paludicella must be regarded as homologous with it. The central circular hole in the cuticula of Zoöbotryon is from 7 to 10 μ in diameter, and from one ninth to one seventh that of the entire plate. Similar

10. Rôle of the Mesodermal Vacuolated Cells.

Allman ('56, p. 36) observed that at the time a lateral branch was well formed, and before the origin of the polypide, the internal outline of the body wall was uneven, and he figures (Plate XI. Fig. 4) very large cells lying on the inside of the body wall. Korotneff ('74, Taf. XII. Figs. 1–3, '75, pp. 369, 370) progressed a step farther, and recognized a distinction between large, coarsely granular cells projecting into the cavity of the bud, especially near the tip, and the surrounding epithelial cells. Braem ('90, p. 126), finally, has described them more accurately. He finds cells filled with numerous granules in the youngest branches of the colony. Immediately around the bud, such cells are less abundant; probably, he says, because their granules have been absorbed in the process of formation of the polypide. He compares the granules with the yolk spherules of the statoblast cells, and believes that they are to be regarded as food matter.

My observations and conclusions, achieved independently of Braem's, fully confirm his. I have succeeded, moreover, in obtaining some additional evidence as to the function of these cells, a subject to which I have paid some attention.

First as to the *distribution* of the cells, and their frequency in different regions. We can best get an approximate idea of this by counting the number of the reticulated cells in each section of a series which involves a young polypide and the regions immediately above and below it. It is not possible to do this with perfect accuracy, because there is no sharp line of distinction between reticulated and non-reticulated cells; but I have made the count without prejudice, and I believe as fairly as possible. When the bud of the polypide has reached about the stage shown in Plate III. Figure 28, the number of reticulated cells seems to have nearly reached a maximum. In the series from which this figure was taken there was an average of 4.8 reticulated cells to the section in the ten sections distal of the bud. There was an average of 11.2 reticulated cells to the section for the twenty sections which passed through the bud, and 11.2 for the eleven sections proximal of the bud in the region

perforated organs have been described by Smitt ('67, p. 426), Nitsche ('71, pp. 420–422), and Vigelius ('84, p. 26) for Flustra, by Freese ('88, p. 7, 13, 14) for Membranipora, by Ostroumoff ('86^a, p. 13) for Lepralia, by Claperède ('70, p. 160) for Bugula and Scrupocellaria, by Ehlers ('76, p. 14) for Hypophorella, and by Joliet ('77, p. 222) for Bowerbankia. Nitsche alone ('71, p. 455) has had anything to say upon their origin, and this apparently not the result of direct observation.

at which muscle fibres were arising. A similar series through a slightly older bud gives for the same regions respectively 5, 14, and 13 cells per section. In series through older buds, a rapid decline in the number of these cells occurs so that at the stage of Figure 30 (Plate IV.) there is an average of only about 3.1 cells per section through the bud, and about 2.2 immediately below. These reticulated cells are not very numerous in the region of the bud at the time this is about to arise, as a look at the sections Figures 3 and 4 shows. One finds reticulated cells in the mesoderm at the tip, and most abundantly at a rather early stage in the development of the bud. The number of these cells diminishes as one leaves the young individual to pass into the next older of the same branch. In the adult such cells are rather rare; so rare, in fact, that Kraepelin ('87), who studied with care the body wall of the adult individual, makes no mention of them. Nevertheless they do occur in the cells which are to go into the lateral branch (Plate II. Fig. 15), as well as elsewhere on the body wall. The place in which one finds the reticulated cells most abundant, however, is in the young *lateral* branches near the time when the polypide bud is about to arise. Here every cell of the mesoderm is greatly enlarged, and filled with the vacuoles (Plate VI. Fig. 58). These are very apparent upon a surface view of the branches. Reticulated cells occur not only in the mesodermic cells of the body wall, but also in those of the polypide bud, which were, indeed, only lately a part of the mural mesoderm (Plate III. Fig. 28, Plate VI. Fig. 56). Thus, in general terms, we may say that the reticulated cells of the mesoderm are chiefly confined to regions in which there are young buds developing; and since these arise at intervals only, there is a periodicity in their appearance, — a time of maximum development followed by one of decline, then one of reproduction of such cells in the ends of branches culminating in another maximum, and so on.

Turning our attention now more particularly to the *structure* of these reticulated cells at the period of their best development, we find (Plate VI. Figs. 56, 57, 59) that they possess a large nucleus lying at the deep end of the cell and containing a relatively large nucleolus, and that this is surrounded by a granular protoplasm with included vacuoles. It is very common to find the nuclei in various stages of division, and thus it is frequently seen as a mass of chromatic substance without any nuclear membrane or nucleochylema. The vacuoles, which in the more regular cells lie in a semicircle nearly peripheral (the nucleus being at the centre), are highly variable in number, some of the cells containing as many as 20 to 30. They often appear as perfectly clear homogeneous spaces, but more frequently at this stage contain a spherical body, which frequently fills the entire vacuole and is more refractive than the surrounding plasma (Fig. 59). Not unfrequently one sees a less refractive, clear space, surrounding the highly refractive body (Fig. 57).

The description just given corresponds to the condition seen in a terminal branch whose polypide has attained the development of that shown in Figure 28 (Plate III.). At the time immediately preceding the origin of the bud, the cuboidal cells of the mesoderm show traces of vacuolation, but their form and size have suffered no appreciable disturbance. This vacuolation of cells proceeds hand in hand with the development of the bud, and one first notices the homogeneous, highly refractive bodies in the vacuoles when the bud is well established. At about the time the alimentary tract has become formed, the reticulated cells begin to show signs of degeneration. The highly refractive bodies have disappeared, and the skeleton of the cell which remains becomes very irregular. As already stated, the number of reticulated cells also decreases, until, at about the time of "rotation" of the polypide, there are few reticulated cells in the mesoderm, but these few are filled with vacuoles and their highly refractive bodies.

The conditions of the mesodermal cells at the tip are slightly different from those found elsewhere. Usually, instead of many small vacuoles, one finds only one or two which fill almost the entire cell, — sometimes perfectly homogeneous in structure, sometimes containing small highly refractive granules.

These appearances I believe to be explicable only upon the assumption that *the mesodermal cells are capable, at the time at which the young polypide is arising, of imbibing the fluids of the body cavity and storing them up for the purpose of supplying the rapidly growing cells of the bud with nutrition.* It is desirable to show reasons for believing, first, that the contents of these cells are nutritive matter; secondly, that this has been taken up from the body cavity; and, thirdly, that it is supplied to the bud for its nutrition.

It must be admitted that the strongest argument for the belief that these are absorbing cells is derived from a comparison of the appearances which we find in these cells with those described for Protozoa, and by Metschnikoff ('83, Taf. I. Figs. 18–35) for mesodermal trophic cells. At the same time, it must be acknowledged that similar cells are found in other cases where the function is believed to be not ingestive, but excretory, as in the chlorogogen cells of Annelids, as shown by Kükenthal ('85), Eisig ('87, pp. 751–762), and others, and indeed even in the cells of cœlomic epithelium. Eisig ('87, p. 752) has already clearly expressed how, in view of the many cases of high excretory activity of peritoneal and blood cells demonstrated by him, "künftighin bei der Beurtheilung gewisser Zelleneinschlüsse erst genau festzustellen sein wird, ob man est mit *von aussen aufgenommenen* (gefressenen), oder aber mit von der Zelle *ausgeschiedenen* Producten zu thun habe."

A criterion for judging this matter may be found, in the first place, I believe, in this: that the products of excretion increase with the activities of the cells, and are thrown out, usually in the shape of concrements, either *from* the cell or *with* the cell into the cœlom; whereas bodies taken in from without for digestion decrease with the activities of the region. In the second place, vacuoles are less characteristic of excretory tissue than of imbibitory. But vacuoles are the important feature of the reticulated cells in Paludicella, and the highly refractive bodies are less constant phenomena. As for the latter, they are not found in the later stages, nor in the earliest. Moreover, these bodies differ from excretion concrements in this, that they are always transparent, often almost indiscernible in the vacuole, except by their higher refractiveness, and there is no sharp demarcation between cases of vacuoles filled by such bodies and those the contents of which are less highly refractive. The degree of refractiveness is variable, at one end of the series grading off into the undifferentiated fluid of the vacuole. What significance is to be assigned to these highly refractive bodies in the vacuoles? There are two reasons why I do not believe that they represent solid food particles devoured as such by the mesodermal cells. First, I do not find such highly refractive bodies lying loose in the body cavity before the stage at which they first appear in the cells; and, secondly, one can find all gradations between less highly refractive vacuoles and highly refractive ones (which I have assumed to be entirely filled by one highly refractive body), and between the latter and vacuoles containing a small body surrounded by a broad, clear area. I believe, therefore, that the vacuoles are rather cavities filled with chemically different nutritive fluids, which are acted upon differently by the reagent.

I have assumed that the contents of the vacuoles represent material taken up from the body cavity, because it seemed most reasonable to look there for the source of their supply. The ectoderm is covered on its outer surface by an apparently continuous cuticula, so that food cannot be gained from the outside world directly. It is, moreover, not unreasonable to suppose that some of the products of digestion elaborated by the adult polypides of the colony pass through the wall of the alimentary tract in solution, and thus into the body cavity, from which they may be taken up by the mesodermal cells at the growing part of the body wall. Nor is there anything unreasonable in insisting that the body cavity functions, in these animals without blood-vessels, as a hæmo-lymph system, for in many animals with incomplete vessels, such as Arthropods, Hirudinea, etc., it evidently does so to a certain degree. Moreover the constant motion of the fluids of the body cavity of Bryozoa points to the same thing. It is conceivable that the food in the digestive cells might be distributed throughout the body wall without passing into the body cavity, since all parts of the body wall are continuous with the digestive epithelia of the polypides of the colony. Two considerations make it improbable that the cells of the tip gain their nutrition in this manner from the digestive cells of the youngest functional polypide: first, the considerable distance of the rapidly growing, and hence rapidly consuming tip, from the youngest functional polypide; and, secondly, the fact that the tip is separated from that polypide by one or two septæ, whose central cells are highly metamorphosed, and apparently cuticularized, thus serving to break the continuity of the cell wall. An objection to the assumption that the mesodermal cells of the tip derive their nourishment from the products of digestion which have been elaborated by the alimentary tract of the youngest polypides and passed into the body cavity, might be based on the fact that the communication plates are always fully formed between the bud and the next older polypide before the older polypide has become functional. If the communication plate were a closed septum, this would be a fatal objection. But it is not closed to fluids carrying food in solution. The very persistence of an opening indicates that it has a function, and favors the hypothesis here presented.

Positive evidence for the conclusion that the reticulated mesodermal cells take up food material from the body cavity is derived from the fact that these cells often show evidences of being amœboid. Thus they are sometimes found with pseudopodia-like prolongations of the cell body (Figs. 54 and 59). A large percentage of all reticulated cells of this stage show similar appearances. Although they here seem to keep their places in the mesodermal epithelium, their movements being confined to their free surfaces, the cells derived from the homologous layer in marine Bryozoa are migratory. Therefore these may be considered as morphological equivalents of migratory cells, which have come to remain in or have never departed from the mesodermal layer, although possessing some of the characters of these notoriously trophic elements.

That the nutritive matter in the cœlomic cells is supplied to the young bud is what we should expect, since the cells of the bud, being most actively engaged in growth, will require most nutriment. The actively dividing cells of the outer layer of the bud are thick and cuboid, and are rarely so highly vacuolated as the more passive ones of the body wall; yet occasionally one finds one or two huge cells in this layer full of vacuoles, which contain highly refractive bodies. In most cases these cells send out processes into the cœlom, and in a few instances I have seen them united with similar processes from cells on distant parts of the body wall. This remarkable phenomenon, shown in Figure 54 (Plate VI.), may possibly signify that cells of the cœlomic epithelium at times directly communicate with those of the outer layer of the bud to supply it with nourishment. Nutrition of the bud is also probably effected through the presence of large reticulated cells at the angle between the bud and the body wall. A condition like that shown in Figure 56, *cl. ret.*, is very common.

Every author from Dumortier et van Beneden to Braem, who has studied the origin of the polypide in Paludicella, has mentioned the presence of highly refractive bodies in the alimentary tract at the time of its formation. These are very striking in *some* living specimens, and in whole animals after killing. I have found that this highly refractive substance in the bud is exceedingly variable in amount and position, and that sometimes it is apparently absent. When present, it usually occupies the lumen of the forming alimentary canal; but, as sections show, it is often located in large vacuoles in the future digestive cells of the alimentary tract. It seems highly probable that, as Braem suggests, this is nutritive substance, and it has doubtless come from the body cavity through the agency not only of the outer layer of the bud, but also of other parts of the cœlomic epithelium.

I am inclined to interpret the phenomenon of cells filled with nutritive material as an adaptation to the peculiar conditions of Paludicella, in which the individuals are early separated from one another, except for the communication plate, through which at best fluids can pass only slowly, and in which a rapid growth of the body wall to produce the polypide takes place periodically. The mesodermal cells rapidly absorb the nutritive fluids of the body cavity and store them in their substance before the formation of the communication plate, and give them out again during the period of the polypide's most rapid growth chiefly to this part of the individual. This hypothesis has been mainly derived from considering the fact of the great development of the reticulated cells in the lateral bud and the very early completion of its communication plate, the immediate needs of the polypide, which arises only after the formation of the plate, being met by this supply of stored nutriment.[1]

But why is the septum (communication plate) formed so early, if it is desirable for the species that the growing tip should be well nourished by the fluids of the body cavity? Here again I must resort to pure hypothesis. I assume that the early formation of the septum is a provision for the protection of the stock against a rapid influx of the surrounding water in case the branch is broken. One can understand how, if the body wall and growing regions depend upon the fluids of the body cavity for nutrition, an open communication of this cavity with the outside world would be a serious obstacle to regeneration of the body wall in the lost part, or the growth of the stock in any other direction. There is a fact which ought to be mentioned in this connection, as bearing on this hypothesis of the function of the septæ. One frequently finds that in stocks which have been handled with reasonable care the median branches are broken off at either end, and in almost every colony one or more lateral branches are missing from the parent branch. Apparently, then, the lateral branches are unusually subject to destruction, and we find the septæ developed at a much earlier period between them and the ancestral branch than between individuals of the median branch. Compare Plate II. Figure 14, in which the communication plate has not yet begun to form, with Plate VI. Figure 58.

III. Budding in Marine Gymnolæmata.

1. Architecture of the Stock.

I have already described the process of stock-building in Paludicella, and have attempted to show that it follows a certain law. I desire now to present a few observations upon the architecture of certain stocks of marine Gymnolæmata, which will aid in arriving at some general conclusions later on. Other observers have worked out the architectural laws of single species or groups, and I shall refer to their studies either in connection with the species which I have used in common with them, or in the general part of this paper, in considering the process of budding in Bryozoa as a whole.

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[1] Similar conditions to those in Paludicella exist in some marine Bryozoa, and in one of these cases, Bowerbankia, I find them fulfilled by a similar arrangement. The young buds of the stolon which give rise to the "nutritive zoöids" are, at an early stage, loaded with food granules. As in Paludicella, so in Bowerbankia the communication plates are formed early.

I will begin my description with *Bugula turrita*[1] of Verrill, which I gathered in the summer of 1889 at Wood's Holl, where it occurs abundantly on the piles of the wharf. The stock is bushy, and, when its polypides are active, of an orange color. In its simplest form the stock consists of a central axis, which is somewhat zigzag, and gives off lateral branches like the trunk of a tree. The lateral branches are inserted on the trunk in a spiral line. Each lateral branch is fan-shaped (Plate VII. Fig. 64), the part corresponding to the handle of the fan being the point of attachment, and the fans are smaller the nearer they are to the tip of the trunk. The attachment of the branch to the trunk is effected by one primary individual. Each fan-shaped branch extends from its point of attachment obliquely upward and outward, and, although it is slightly concave on its upper inner surface, the concavity is not sufficient to prevent its being spread out upon the slide for study without materially disturbing the interrelation of the individuals in the stock.

I have studied several branches flattened in this way (one of 400 individuals), and have made camera drawings of them. Since the results in the different cases are substantially in agreement, I have concluded that they are significant. One of these camera drawings is shown in the figure just referred to.

To designate individuals in the stock, I have adopted a simple nomenclature. The forty-four terminal individuals are numbered from 1 to 44. The successive generations (if I may be allowed to use this word in a loose way) are indicated by the Roman numerals from I. to XIII. Any one individual is indicated by placing the numbers of the radial line or lines to which it belongs first, and following this by the Roman numeral of the generation to which it belongs. Thus, 27–30 IV. is an individual near the base of the twig 27–30 and of generation IV. Figure 64^a (Plate VII.) is a diagram showing the arrangement of the individuals in Figure 64. The radial lines represent the rows of individuals; the concentric lines separate adjacent individuals of the same radial row. The same nomenclature is used as in Figure 64.

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[1] This species is very similar in general habit to B. avicularia, Linnæus, and to B. turbinata, Alder (Hincks, '80, pp. 75–80). It differs from the first named species by possessing only one spine, on the outer upper edge, as described by Leidy ('55, p. 142), instead of having three, — two outer upper and one inner and upper. It differs from Hincks's diagnosis of the second in having only two "cells" in each branch, instead of 3–6 in the upper portions. The form of the avicularium would seem to ally it more closely to B. avicularia.

In studying Figures 64 and 64^a, one of the first facts which attracts our attention is that (1) *the individuals of the twigs are in pairs, and the adjacent individuals of the two rows "break joints."* In general, one finds that the individuals of the same twig are of the same length; but since the two rows of any twig ultimately rest upon one, either the proximal two individuals of these rows must be of unequal length, or else they must arise on different parts of the individual which supports them. Both of these cases occur. Sometimes one individual (26 IX.) has nearly twice the length of the other (25 IX.), and in other cases (9, 10 VI., 11, 12 VI.) the more proximal of the two individuals (9, 10 VI.) arises so far proximally on the side of the supporting individual 9–12 V. as to have a total length quite equal to that of the more distal (11, 12 VI.). Owing to their different positions upon the individual 9–12 V., these two individuals may be designated as lateral (9, 10 VI.) and terminal (11, 22, VI.). *The terminal individuals continue the ancestral row; the lateral individuals are the first of lateral branches.*

This distinction is an actual, and by no means a meaningless one. The constant difference in position of the two individuals which rest upon one shows conclusively that this branching cannot be regarded as dichotomous, and I may say parenthetically that I shall try to show in the general part of this paper that true dichotomy is not common in Bryozoan stocks, if indeed it exist at all. Now, since in the rows of individuals in which there is no lateral budding the distal lies directly terminal to the proximal individual, that individual which fulfils this condition at the region of bifurcation of the twig must be regarded as continuing the ancestral branch; and that individual, conversely, which arises from the side of the single proximal individual must be regarded as the lateral one. Thus we have the stock composed of ancestral and lateral branches as represented in Figure 64^a.

(2) *When two lateral branches are given off from two ancestral ones which have had a common origin* (and are consequently themselves respectively ancestral and lateral branches), *they are given off towards each other.* This is equally true whether the two lateral branches in question arise in the same generation (32 X., 33 X.) or in different

generations (24 X., 25 IX.). This may be expressed by saying branches are given off on the side towards the axils.

By consulting Figure 64^a and tracing out the finely dotted lines which connect the second, third, etc. axils of all branches counting from the proximal end of the fan, it will be seen that (3) *lateral buds tend to arise on two closely related branches in the same generation.* There are several slight deviations from this rule. The less closely related the branches, the less marked the tendency, although it is still discernible. (Cf. branches 9–16, 23–30.)

This rule does not hold, however, so well on the margins as in the middle region of the fan, for here another and a superior rule seems to obtain. This is that (4) *lateral budding occurs more frequently at the margins of "fans" than elsewhere.* Thus in Figure 64^a there is at the margins, on the average, 1 case of lateral budding to 4.3 cases of median budding. Elsewhere the average is as 1 to 6.5. In larger fans the difference is even more pronounced. This is true not only for the "fans," but also, to a less degree, for the two "subfans" which arise respectively from the two individuals of generation II. (but 17, 18 is very anomalous in this respect). In general, any rule deduced for the margin of the fans holds true also for subfans to any degree of subdivision; but the less perfectly, the higher the degree.

By consulting again the diagram, it will be seen that the branches have attained different lengths. Thus 9, 10, 29, and 30 contain representatives of generation XIII., while the terminal individual of branch 1 is of generation X., and those of branches 35–44 are of generation XI. So the curve which connects the tips of the branches (see dot-and-dash line, Fig. 64^a) would rise from 1 to 9–10 as a maximum, and fall again till it reached the margin of the first subfan; then rise again, reaching a second maximum in the middle at 29–30, and finally fall again to the other margin. In general, then, (5) *the marginal branches are shortest, the intermediate ones longest,* i. e. *give rise to the greatest number of generations.*

Although the marginal individuals of say generation III., IV., or V. do not support branches with so many generations as the intermediate ones, yet they are not therefore necessarily less prolific in individuals, because the number of branches arising distally of such individuals is greater according to rule 4 than the number arising distally of the intermediate ones. Thus, if we count the number of individuals borne on each of the eight individuals of the fourth (IV.) generation of Figure 64, we find in the given case: —

Outer.	1.	1–8 IV. (an outer	individ.)	gives rise to	8	branches and	34	individ.
	2.	9–12 IV. (an inner	“)	“ “	4	“ “	27	“
Inner.	3.	13–16 IV. (an inner	“)	“ “	4	“ “	23	“
	4.	17, 18 IV. (a subouter	“)	“ “	2	“ “	13	“
Inner.	5.	19–22 IV. (a subouter	“)	“ “	4	“ “	25	“
	6.	23–26 IV. (an inner	“)	“ “	4	“ “	23	“
Outer.	7.	27–30 IV. (an inner	“)	“ “	4	“ “	26	“
	8.	31–44 IV. (an outer	“)	“ “	14	“ “	56	“

According to the rule that inner branches are slightly prolific, we should expect cases numbered 4 and 5 in the above table to contain the fewest branches and individuals; in accordance with the rule that marginal branches even of subfans are more prolific, we should expect them, on the contrary, to contain more branches and individuals than cases numbered 3, 6, etc. The result is usually a condition intermediate between that of the middle and outer branches, such as is partially realized in case number 5. Case number 4 seems to present an unusual condition, which may be correlated with the fact of its close approximation to number 5. (See Fig. 64, 17–20.) From the consideration of this and other cases, I think this conclusion may fairly be drawn: (6) *Of the four proximal individuals from which a fan arises, the outer two will bear the greater number of individuals, the inner two the lesser.*

Since from rule 2 median individuals (ancestral branches) occupy the margins of fans (or subfans of any degree) and the lateral branches are intermediate, it follows, as a corollary to rule 5, that, in general, the ancestral branches are the shorter, the lateral branches the longer; and, as a corollary to rule 6, that from any axil the ancestral branch will of the two give rise to the greater number of individuals; the lateral branch, conversely, to the less, other conditions being equal.

We have deduced the laws of lateral budding on different parts of the circumference. We find also that there is a regular variation in the frequency of lateral budding, dependent upon the distance of the region from the primary individual of the fan. This rule, like any other, is not invariable, whatever the other conditions may be; but it is more or less dependent upon them. A small and regular fan having seven generations gives this result.

No. of Generation.	Number of Individ.	Increase per Cent.
I.	1	
II.	2	100
III.	4	100
IV.	8	100
V.	12	50
VI.	16	33⅓
VII.	16	0

In this table the first column gives the number of the generation, the second the whole number of individuals in the generation, and the third column the increase per cent of individuals in each succeeding generation over the last. In this specimen the increase underwent a very regular diminution.

With larger colonies so great a regularity as that just shown is hardly to be expected, nor is it found. The following table is based on Figure 64, and is like the preceding; but in addition the percentage increases have been averaged — i. e. the means of successive increases taken in pairs have been given — to eliminate what may be called accidental variations.

Generation.	Number of Individ.	Increase per Cent.	Average.	Generation	Number of Individ.	Increase per Cent.	Average.
I.	1						29
				VIII.	28	27	
II.	2	100					23
			100	IX.	33	18	
III.	4	100					18
			100	X.	39	18	
IV.	8	100					16
			88	XI.	44	13	
V.	14	75					
			49	XII.	20	Incomplete.	
VI.	17	22					
			26	XIII.	4		
VII.	22	30					

Hence we conclude, *There is a diminution in the rate of increase of individuals in the "fan" as it grows older.*

In searching for an explanation of this phenomenon, I first drew a line from the centre of the primary individual of the fan to the periphery, and divided it into four equal parts. I then described arcs with the primary individual as a centre, and with radii equal to $\frac{1}{4}$, $\frac{2}{4}$, $\frac{3}{4}$, and $\frac{4}{4}$ of this line respectively. Counting the number of individuals cut by these arcs respectively, and dividing those numbers by the length of the corresponding arcs, I found that *there is almost exactly the same number of individuals per unit of arc for each of the four arcs.* (Rule 7.) The previous conclusion, that there is a diminution in the rate of increase of individuals in the fan as it grows older, may then be considered as a corollary to this rule, as it obviously follows from it.

Bugula flabellata, J. V. Thompson.[1] — I have studied this species for the purpose of confirming the results obtained in B. turrita, and have found the architecture of the two species alike in all essentials.

The entire colony of B. flabellata (Plate VII. Fig. 66) may be compared to a single "fan" of B. turrita, only there are usually many more individuals in the former, and of course there is no central stem to which it is attached; but the fan is fastened directly by its rhizoids to the object which supports it.

Usually about four rows of individuals are united, instead of two as in B. turrita, — a condition which can be easily derived from the latter by imagining adjacent branches to become fused together. Here as there adjacent individuals break joints. Here as there lateral branches are given off towards the axils.

Rule 3 is not true for B. flabellata. This is entirely annulled by the establishment of a new rule, which depends upon the new conditions found in this species; namely, that more than two rows cling together, and that consequently one or more rows of individuals are enclosed between outer marginal rows. In any such twig composed of more than two rows (Rule 3a) *lateral branches are given off only from the marginal rows.* (See Fig. 66, 49–54 XVII.) It might possibly result, then, that certain of the middle rows of the twig should never give rise to lateral branches. But I do not believe that this ever occurs in very long rows, for by the splitting up of the twigs the middle rows sooner or later become marginal (so 46–51 XV.). In one stock that I have drawn, consisting of 17 to 21 generations, every middle row occurring as such up to the 13th generation had become at the periphery a marginal row.

As in B. turrita, so in B. flabellata lateral budding occurs most frequently at the margins of fans, — in a fan of about 800 individuals in the ratio of 1 : 10 for the margin, and 1 : 14 for the remainder of the fan. By a comparison of these figures with those given on page 43 for B. turrita, it will also appear that lateral budding is less frequent here relatively to terminal budding than in B. turrita.

The fifth rule deduced for B. turrita holds equally well here. In one case the curve of the tips of the rows rises from the margin of the fan at generation XXIV., reaches 3 maxima of XXVI., XXVII., and XXVIII. respectively, and falls again at the other margin to generation XXIII. In the subfan from which Figure 66 was taken, the curve begins at the outer margin with generation XVII., rises to generation XXII. at two points, and falls again to XX. at the inner margin of the subfan.

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[1] The species which I have studied is identified by Verrill ('73, pp. 711, 389) under this name, and my specimens also agree fairly with Hincks's ('80, pp. 80–82) diagnosis. The two pairs of spines, one longer than the other, could be distinctly seen. Hincks says, "The rows of cells . . . are never, I believe, fewer than four, and range as high as seven." But his Figure 66 shows three rows only in some places.

Of the four proximal individuals in any fan here, as in Bugula turrita, the outermost, ancestral give rise to the greater number of individuals. In one case, for instance, the marginal individuals lie at the base of 31 rows with 184 individuals, while the inner ones support only 7 branches with 65 individuals. Similar results were obtained from other stocks.

With the middle of the primary individual as a centre, I passed an arc of a circle through the extremities of the branches of a large camera drawing of a fan of B. flabellata, divided the radius into eighths, and passed arcs through these points. The number of individuals cut by the different arcs was then counted and tabulated; the arc with the longest radius cut through 87 individuals. By measuring the length of the arcs, the number which should be cut by each arc on the assumption that the number of individuals per unit of arc is constant for all radii was determined. This was then compared with the actual number found, with the following results: —

Length of Radius.	No. of Individuals observed.	Theoretic No.	Length of Radius.	No. of Individuals observed.	Theoretic No.
1	3	$2\frac{1}{2}$	5	37	40
2	7	6	6	56	56
3	13	13	7	68	70
4	22	25	8	87	[87]

In this instance, then, the 7th rule deduced for B. turrita evidently holds true for B. flabellata.

While at Mr. Agassiz's laboratory at Newport, during the summer of 1890, I had frequent opportunity to examine other stocks of Bryozoa, which occur there very abundantly. I will take four species as typical examples of the groups they represent, and treat of the architecture of their colonies.

Lepralia Pallasiana, Busk.[1] — It is not at all easy to determine from a young stock what has been the order of succession of individuals. One has to view the object from both sides, make a careful examination of the walls of the zoœcia and of the relation of the polypides to one another, and, when he has done his best to determine what are the facts, he must feel that his conclusions are after all more or less subjective. By a careful study of the colony shown in Figure 71, I have constructed the diagram shown in Figure 71^a.

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[1] I do not feel perfectly certain that the specimen shown in Figure 71 (Plate VIII.) belongs to this species, because the characters of the young stocks differ some-

The stock of Lepralia is a creeping one, and all of its rows of individuals are in juxtaposition. This juxtaposition is continued into the adult stage. Even the young stock begins to show evidence of a quincunx arrangement of individuals. This is less evident in the youngest individuals than in the older part of the stock, and is most evident in old colonies. That there is not here a true dichotomous division of rows of individuals, resulting in the annihilation of the ancestral row and the establishment of two new ones, is evident from a glance at the youngest generation in rows 11, 12, or, better, 2, 3, in which the relation of terminal (11, 3) and lateral (12, 2) individuals is very different. The former continue the ancestral line, the latter establish new rows. Lepralia differs from Bugula in this: that two lateral branches may be given off from the ancestral row in the same generation, as at *B*, *C*, and *a*, *a* (enclosed in circles), Figure 71^a.

In contradistinction to the conditions in Bugula, when only one branch arises, it is not given off towards the axil, but away from it.

The synchronism of the budding process noticed in B. turrita is hardly distinguishable in the adult stock of this species; in the young, however, it is quite marked, and gives to the whole a very symmetrical form. The cleavage of eggs does not proceed by more regular steps. Of the three individuals *a*, *C*, *a* (in circles), which follow *B*, each has given rise to three others, a median and two lateral. From each of the three individuals derived from the two individuals *a*, *a* (in circles) has arisen a lateral branch. Rule 3 is therefore well marked in the young stock of Lepralia.

Rule 4, concerning the greater frequency of lateral budding at the margin, is also exemplified in Lepralia. The ratio of cases of lateral to median budding being 1 : 1 on the margin (rows 1–6 and 15–19) and 1 : 2.8 in the middle (rows 7–14.)

In Bugula, as will be recalled, it was concluded that the marginal

what from those of older ones. Yet it is an Escharine closely allied to Lepralia, and I have seen in some cases the broad-based spine on the proximal border referred to by Verrill as being found in L. Pallasiana.

branches were possessed of fewer generations than the intermediate ones. Since by Rule 2 the lateral branches were given off towards the axils, and the ancestral branches therefore always remained marginal, it resulted that the ancestral branches were the shorter, the lateral branches the longer. But in Lepralia lateral branches are turned away from the axils, and here we find the conditions concerning the relative number of generations in marginal and intermediate rows correspondingly reversed. Thus, in Figure 71^a, the terminal individual *D* of row 10, a median but ancestral row, belongs to generation IV. while the lateral branches 6 and 15 have five generations of polypides. Thus it is true here, as in Bugula, that the ancestral branches are the shorter, the lateral branches the longer (page 44).

That the outer individuals *a*, *a*, of rows 6 and 15, have given rise to more individuals than the inner *C*, is clear without further comment. Finally, since the individuals retain a nearly constant width, the necessity of the rule established for Bugula, — viz. that there is almost exactly the same number of individuals per unit of arc for all radii, — and of its corollary, — that the increase of individuals in sucessive generations undergoes a regular diminution, — is apparent.

Flustrella hispida, Fabricius.[1] — This stock is a very dense corm-like one. The primary individual becomes surrounded on all sides by the younger zoœcia. It is very evident from an inspection of the position of this primary polypide with relation to the periphery, that growth occurs most rapidly on each side and in front of the primary polypide. In making any diagram of such a stock, it is not very difficult to decide upon the origin of the more peripheral individuals of the stock, but it is wellnigh impossible to say with any certainty what are the relations of the individuals of the second generation to those of the first. Barrois ('77, pp. 227–229) has, however, determined this for this species, and my diagram (Fig. 67) is based in part upon his observations. I do not desire to insist that the diagram represents the exact method of growth of the stock. It is an attempt to represent it, founded principally on careful study of Figure 69. The quincunx arrangement of individuals is already apparent in the young stock (Fig. 69); it becomes more evident in the adult, and when new individuals arise distad to any two, one of the new ones is median (ancestral branch), the other lateral. (So terminal individual of rows 11 and 10 ; 22, 23 ; 43, 44 ; etc.) In the diagram, however, I have not always indicated which is the median and which the lateral branch, for in the older parts of the colony, owing to a shoving of individuals, it is not easy to distinguish them.

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[1] Hincks ('80, pp. 504–506) makes the existence of a larval bivalve shell a characteristic of this genus, and therefore I assign to it a very common Alcyonidium-like form which was extremely abundant on Fucus at Newport. F. hispida is the only species of this genus. I found the bivalve shell still adhering to the primary individual of a young colony (Plate VIII. Fig. 69, *o.*). In Verrill's ('73, p. 708) catalogue this species is referred to under the name "Alcyonidium hispidum, Smitt."

Lateral branches appear usually to be given off towards the axis. Here, as in Bugula, the lateral branches tend to be longer ; the ancestral, shorter.

It is evident from the diagram that lateral budding is most frequent at the margins of the corm, i. e. that part lying posterio-dextral or posterio-sinistral of the primary individual, and that the descendants of the two lateral individuals of the four belonging to generation II. are more numerous than those derived from the middle two. Finally, it is evident that the number of individuals per unit of arc will be the same for arcs of all radii, and therefore the rate of increase of individuals will diminish through successive generations.

In *Crisia eburnea*, Linn.,[1] we find the same laws illustrated. The architecture of the genus has been carefully treated of by Smitt ('65^a, pp. 115–142) as forming the basis of classification. Barrois ('77, pp. 76–85) has described in a masterly way the formation of the young stock of tubuliporid Cyclostomata, and the relationships of the different types of budding in this group. Harmer ('91, pp. 145–173) has recently discussed the architecture of the stock in British species, adopting Smitt's graphic method of showing it. I have found his paper of great value for my purpose.

This species grows as a shrub-like stock upon floating eel-grass, etc. I was wrong in saying, in my Preliminary ('91, p. 282), that Crisia has its branches united in pairs. The comparison of this species made by Barrois ('77, p. 82) with the "geniculata form" is conclusive evidence, to my mind, that the apparent double row is in reality a single one, and that such a branch as 18, Figure 65, is to be represented by a single line in the diagram Figure 65^a. We find here terminal and lateral branches ; no true dichotomy. Branches are given off on the side *away* from the axils, as in Lepralia, not as in Bugula. (But branch 11 is an exception to the rule.) They are given off, as Harmer ('91, p. 131) has shown, alternately to the right and left.

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[1] This is the only species of Crisia given by Verrill, and, since my species is very common, it must be the one to which he refers. Moreover, it agrees fairly well with Harmer's diagnosis ('91, p. 131).

There is something of a tendency for lateral branches to be given off in the same generation from closely related branches. Thus (Fig. 65^a) from the primary individual, *o*, of the stock, two individuals, a median and a lateral one, arise. Each gives rise in its first generation to two individuals, a median and a lateral. Of these four individuals each gives rise at the end of three generations of median buds to two buds, a median and a lateral. Comparing 2 and 10, first descendants of the two branches arising from the second individual of 8, we find that each gives rise to lateral branches from their first individual and from their fourth. Comparing 14 and 19, first descendants of the two branches arising from the first individual of 8, we find each giving rise to lateral branches from their first individuals. The law breaks down, however, when an attempt is made to carry it to extremes.

The fourth rule is not always so pronounced in Crisia eburnea as elsewhere, although lateral budding seems to be slightly more frequent at the margin.

The extreme marginal branches usually attain far fewer generations than the more intermediate ones; thus, in Figure 65^a, branch 20 ends in the 7th generation and branch 13 in the 7th also, while the more intermediate branches 15 and 18 attain 12 and 14 generations respectively. So, too, while the outer branches 6 and 1 contain respectively 10 and 11 generations, the inner branches reach 12 and 14.

It is very noticeable that the outer branches give rise to more individuals than the intermediate ones. Figure 65^a will serve to illustrate this also. Here the outer branch 4, the intermediate 8, and the outer 15 possess, together with the branches arising from them, 33, 28, and 40 individuals respectively. Harmer ('91, p. 168) finds this true for his Crisia ramosa, for he says, "It is frequently remarked that the longest and most branched parts of the colony are lateral branches, and not parts of the main stems."

There is, in the long run, a decrement in the rate of increase of individuals in successively older generations, yet it is not so regular a one as that which we found to exist in Bugula. Thus, in the seven generations which even the shortest branches shown in Figure 65^a had attained, the average increase of the number of individuals in the second, third, and fourth generations over the number in the preceding is 67%; in the fifth, sixth, and seventh, 44%. The generations beyond the seventh are not complete; they would have contained more individuals at a later period, when the branches which have now attained only seven generations had grown. Thus the number of individuals in successive generations beyond the seventh increases more and more slowly, and finally decreases to zero. Thus the average rate of increase of individuals in the generations 7 to 10 over those in the preceding is only 16%.

One finds here, as elsewhere, that the number of individuals cut by any unit of arc, the primary individual being taken as a centre, remains practically constant, whatever the radius of the arc.

In studying the creeping stocks of Cheilostomes (Plate VIII. Fig. 71), young corms have been chosen because they exhibit fewer irregularities of formation than old ones. Such irregularities are chiefly due to some unevenness of the surface on which the corms lie, but sometimes apparently to a crowding of individuals. Old rows of individuals are occasionally entirely cut off and end in the middle of the stock; sometimes two rows running side by side, perhaps derived from a common ancestor, suddenly merge into one again. In one case, Escharella variabilis, Verrill, I have seen three rows thus merge into one at the margin, suggesting the existence of a *samknopp* (common bud) in the sense of Smitt ('65, pp. 5–16). Ostroumoff ('86^a, pp. 338, 339) has observed a case in Lepralia Pallasiana. He says: "Dans quelques cas, qu'on peut considérer comme des anomalies, il arrive parfois que deux bourgeons, provenant de loges différentes, viennent à se fusionner." It seems to me, therefore, that while Nitsche ('71, pp. 445, 446), who opposed with such vehemence and success the idea of Smitt that zoœcia arise from an undivided marginal zone of cells, was quite right in affirming ('71, p. 447) that even the smallest marginal zoœcia are sharply marked off from the adjacent ones, yet he overlooked the possibility that under certain circumstances the lateral walls might fail to develop, and thus one zoœcium might arise in the place of two, or even three.

I have not read Smitt's Swedish paper, but I do not find anything in the translation given by Nitsche to warrant the latter's conclusion ('71, p. 446) that Smitt believed the "Gesammtknospe" to be "formed from the sum total of the mature peripheral zoœcia." If I understand Smitt, he conceived the *samknopp* not to be derived from the most peripheral mature zoœcia, but to be self-proliferating, and to give rise to the rows of zoœcia, not to arise from them. It is the "bud of the colony," not the sum of the buds of the peripheral individuals of the stock. In this I would agree with him exactly. Although *usually* one finds the marginal gemmiparous tissue forming the lateral walls at the extreme edge of the corm, and thus apparently separated into wholly distinct adjacent gemmiparous masses; under certain conditions, the lateral wall may not be formed between two or more rows, which will then merge into one.

2. Origin and Development of the Individual.

My studies on this subject, which were undertaken for the purpose of showing the unity of the type of budding throughout Ectoprocta, have been very fragmentary.

Figure 72 (Plate IX.) has been introduced for the sake of orientation. It represents a longitudinal vertical section through the peripheral part of a stock of Lepralia Pallasiana. The body wall is thicker at the margin (*marg.*), and gradually becomes thinner as one passes backward. A septum (*sep.*) has already arisen cutting off the youngest zoœcium from the more proximal one, which contains a young polypide; proximal to this is another septum, and the distal end of a third zoœcium.

Nitsche ('71, pp. 445–456) has already well described the process of forming the *zoœcium* in Flustra membranacea. In fact, he has studied the organogeny more thoroughly in many respects than I have. Nitsche ('71, p. 452) showed that the wall of the advancing margin of the colony was composed of two layers of cells, — an outer, "Cylinderepithelschicht," which secretes a cuticula, and an inner, "Spindelzellschicht mit anliegenden Körnerhaufen." As the body wall formed directly from these cell layers is left behind by the advance of the margin, it becomes continually thinner. "Die Cylinderepithelzellen der Wandung platten sich weiter nach dem proximalen Ende zu ein wenig ab, besonders die der Unterseite verkürzen sich, die einzelnen Zellen rücken auseinander, die Zellgrenzen werden undeutlicher, die Kerne jedoch bleiben deutlich erkennbar." Vigelius ('84, p. 76) could not find the inner cell layer in Flustra, even at the youngest stages, and consequently he believed that only one existed at the margin, and that this went to form the "*Parenchymgewebe*" of the adult. Ostroumoff ('86^a, p. 336) seems inclined to doubt the existence of any mesodermal *layer* at the distal portion of the budding zoœcium in Cheilostomes, and Seeliger ('90, p. 580) has failed to find in Bugula "eine *zusammenhängende* dem Ectoderm dicht anliegende Schicht von mesodermalen Spindelzellen." Both Ostroumoff and Seeliger, however, believe in the existence of *isolated* mesodermal elements at the budding end.

According to my own observations, there is usually only one continuous layer at the budding margin of the stock. Thus, in Flustrella (Plate IX. Fig. 79) one can usually distinguish a continuous ectoderm, but the mesoderm (*ms'drm.*) is represented by scattered cells only. At the margin in Lepralia (Fig. 73) one finds a thick ectodermal layer, composed of columnar cells, but the mesoderm consists of an irregular thick mass of cells, some of which appear to be amœboid. They however show no signs of having been derived from the outer layer. The condition of the budding margin of Escharella resembles that of Lepralia. In older parts of the body wall, where the ectoderm is reduced to an extremely thin layer, only scattered mesodermal cells appear, and these are amœboid or mesenchymatoid.

On the other hand, one finds in the body wall, around the nascent neck of the polypide (Plate X. Fig. 88), even to a late stage, both ectoderm and mesoderm well formed as *layers*. The ectoderm is a columnar epithelium; the mesoderm is flatter, and often its cells are not sharply delimited from one another. It is thus perfectly evident, to my mind, that the mesoderm has in general lost its original epithelial character in the marine Bryozoa, although it has retained it in Phylactolæmata. Whenever it does exist in the former group as an epithelium, it is at the budding regions (neck of polypide, and Figures 74, 75, 78, 79, *ex.*).

Origin of the Polypide. — There are very few problems in modern morphology, I fancy, the history of whose investigation shows a less satisfactory aspect than that of the origin of the polypide in Gymnolæmata. It is hardly to be wondered, however, that investigators have sought for another interpretation of the process than the most obvious one, because that seemed to oppose many long cherished and wellnigh universally held dogmas. While the first recognition of the animal nature of marine Bryozoa, which we owe to the studies of Bernard de Jussieu in 1742 and John Ellis in 1755, brought with it a knowledge of their colonial nature, yet it was not until much later that the most characteristic part of this process — the formation of the polypide — was clearly observed. Grant ('27, p. 115) and Farre ('37, pp. 400, 409, 415) first described the process by which is formed this complex of organs, and settled once for all the controversy which had sprung up as to whether these animals were truly stock-builders. Under the influence on the one hand of the endosarc theory of Joliet ('77), and on the other hand of the view promulgated by Hatschek ('77), that similar organs in larva and polypide are equivalent as far as regards their origin from the germ layers, the more important papers [1] between '77 and '90 maintained either that the polypide arose independently of the body wall, and secondarily acquired connection with it, or that it had a double origin.

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[1] Excepting those of Barrois, who, from the study of the favorable material presented by metamorphosing larvæ, has persistently maintained the correct interpretation.

To Nitsche ('71, pp. 456–463) belongs the credit of having first described the histological changes in the origin and development of the polypide of marine Bryozoa, particularly with reference to the part which the germ layers play in that process. He says ('71, p. 456): "Die Anlage des Polypids erscheint zunächst als eine Wucherung der Zellschicht der Endocyste in der Mitte der Hinterwand der Knospe, und zwar in dem Winkel, den die Hinterwand mit der oberen Wand macht. Bald ordnen sich die Bestandtheile des regellosen Zellhaufens in zwei deutlich gesonderte Schichten, und wir sehen nun einen rundlichen Körper, bestehend aus einer äusseren einschichtigen Zellschicht, welche sich scharf absetzt gegen die das Innere des Körpers bildenden Zellen."

This stood until a year ago as the most satisfactory description of this process in the adult stock. The appearance within the last year of the two papers of Prouho ('90) and Seeliger ('90) marks a distinct epoch in the advance of our knowledge concerning the origin of the polypide in Gymnolæmata. The paper of Prouho treats of the process in the case of the primary polypide of the metamorphosing larva of Flustrella, that of Seeliger in the case of the young (practically adult) stock of Bugula. According to both authors, the polypide arises from the body wall by an invagination of it, and its two layers are from the first distinct and separate, and go to form the two layers of the adult polypide, and the whole of those two layers. The outer layer of the body wall gives rise to the outer layer of the tentacles and the lining of the alimentary tract, and the inner layer of the body wall gives rise to the mesodermal lining of the polypide. Prouho alone is cognizant of the method of origin of the ganglion, and in addition there are several points of difference between these two authors concerning the development of other organs, to which I shall refer in the proper place. Thus the latest studies have confirmed the assertions of Nitsche, that the polypide arises from a single centre of proliferation of the body wall; they have made an advance in this, that they have shown that the two layers of the bud do not become secondarily differentiated from a single cell mass, but are respectively derived from the two cell layers of the body wall. My own studies have led me to the same conclusion on this point.

Figure 75 (Plate IX.) is a vertical radial section through the margin of an adult Flustrella stock. The ectoderm is relatively thick at the sole (*sol.*) and margin, and very greatly thickened at the point marked *gm.* Here two layers, sharply separated, are apparent. The cells of the outer layer are columnar and full of granular protoplasm, the mesodermal cells cuboid. The body wall has clearly begun to invaginate in this region. Figure 79 is a similar section, and shows a later stage in this process. The lumen of the bud is apparent, and has been formed by invagination, not, as in Paludicella or Phylactolæmata, by ingression. The two layers of the bud are apparent; they have been derived from those of the body wall.

Figure 73 (Plate IX.) shows a stage in the development of the polypide which is intermediate between that of Figures 75 and 79, but from another suborder, Cheilostomata. The mesoderm has here a mesenchymatous character, and is loosely attached to the inner layer of the bud; it is not always sharply marked off from it by boundaries, but is quite distinct in its reaction with staining reagents. This bud has evidently arisen by invagination of the body wall. Seeliger ('90, p. 581) also finds that there is an actual invagination of the ectoderm in Bugula, the opening to which he calls "blastopore."

From what has been already shown, it is evident that in Flustrella, as well as in Cheilostomata, the first appearance of the young polypide is near the margin of the stock, not near the proximal part of the young zoœcium. This will also be apparent at 6 and 9, Figure 71 (Plate VIII.), where the accumulation of nuclei immediately behind the margin indicates the neck of the polypide, — the point at which the bud arose. To be sure, at quite an early stage, but very much later than that of Figure 73, the polypides are found near the proximal wall of the zoœcium, but a delicate funnel-shaped sheath of tissue runs from the polypide to the distal part of the zoœcium, where the polypide is attached to the body wall.

After invagination the pocket closes at its attached end by a growing together of its lips (Figs. 79, 78). Thus the body wall becomes continuous again over the lumen of the bud, and this union is first broken when the fully formed polypide is ready to evaginate itself. Seeliger ('90, p. 582, Taf. XXVI. Figs. 8, 10) has described and figured a similar condition in Bugula.

The young bud now becomes elongated (Fig. 80), the walls of the bud sometimes becoming closely approximated. A little later it begins to pass backwards relatively to the distal wall of the zoœcium. A transverse section through the young polypide and the neck of the colony shows that the connection has become a less intimate one (Fig. 81, *cev. pyd.*). The tissue by which the connection is still effected is that from which the kamptoderm will be formed. It is apparently the existence of this stage, in which the kamptoderm is long drawn out and easily overlooked in optical as well as actual sections, that led to the belief that polypide buds may arise independently of the body wall and only secondarily become connected with it.

At about this time the lumen of the *alimentary tract* begins to be separated from that of the atrium. Thus, in the series from which Figure 81 was taken the more oralward lying sections show that the cavities of the lower and the upper parts of the bud, which at the anal end are broadly confluent, have here become separated by a constriction. A sagittal section of a somewhat later stage is shown in Figure 76, which is from Flustrella. Here we find the alimentary tract represented by a space in the lower part of the bud, broader at its anal than at its oral end and separated from the upper cavity — the common atrio-pharyngeal cavity, *œ.* + *atr.* — by a line of nuclei which represents the line of approximation of the inner layers of the two sides of the bud. The bud is attached to the body wall at its marginal (anal) end, and is free from it oralwards. (Compare with Paludicella, Plate III. Fig. 24.) It seems to me highly probable from these and other series of sections that the alimentary tract is separated from the rest of the lumen of the bud, not by an approximation of the inner layers of the bud along the whole extent of the future alimentary tract at once, but that the rectal part is first formed and constitutes a large cavity, at first broadly open to the atrium above, and that the gastric portion is formed somewhat later by a progressive enlargement of the lower cavity of the bud, which now becomes constricted off from the atrium and œsophagus above. This process is like that found in Paludicella (page 19), which forms a sort of transition to that of Phylactolæmata, described by Braem ('90, pp. 45, 46) and myself ('90, p. 112).

Prouho ('90, p. 448, Fig. 6) shows that the rectum at first appears as a *blind sac* open to the atrium at its posterior end, although later this opening is greatly reduced. Hence in the Flustrella larva also the space from which the lumen of the future rectum is to arise is formed before that of the stomach, although this part of the alimentary tract is the last to be cut off from the atrium. Seeliger ('90, p. 585) says concerning the formation of the alimentary tract in Bugula: "Der ganze Basaltheil des Polypids sich in der Mittelpartie durch zwei immer tiefer werdende Furchen von dem vorderen abschnürt, während er an zwei Stellen, einer oberen und einer unteren, mit ihm in Verbindung bleibt. Die obere Verbindung entspricht dem Anus, die untere dem Mund." The author here seems to imply that the whole alimentary tract is formed at one time ; but as he has not attended particularly to this point, this can hardly be said to militate against my view.

There is, however, in my opinion, a more important error in Seeliger's description of the origin of the alimentary tract, — an error into which Nitsche ('71, p. 457) also fell. As in Phylactolæmata and Paludicella, so also in marine Bryozoa in general, so far as I have studied them, the posterior and anterior parts of the alimentary tract are formed independently, and their cavities coalesce only secondarily. The constriction which separates the lumen of the bud into a cavity nearer, "*vorder*," and one more remote from the body wall, "*basal*," does not separate off the whole alimentary tract from the atrium. Neither does that constriction result in the formation of a space opening into the cavity nearer the body wall, "*Vordertheil*," at an upper [distal] point (anus) and lower [proximal] point (mouth). Thus if one examines a complete series of sections through a polypide even of so late a stage as Figure 92 (Plate X.), one finds that, while there is an open connection between the anal end of the alimentary tract and the atrium, the oral end is at all points sharply separated from the cavity above by a double-layered wall of cells, as is shown in Figure 92, between *œ.* and *ga.* Such a condition, moreover, has been found by Barrois ('86, pp. 73–76) in the primary polypide of Lepralia, and by Prouho, as just stated, in the primary polypide of Flustrella.

Origin and Development of the Ring Canal and Tentacles. — Nitsche ('71, p. 430) first described in Flustra a ring canal surrounding the mouth-opening and lying at the base of the tentacles, but did not refer to the origin of it. Seeliger ('90, p. 588) describes it in a young polypide of Bugula, as derived from the mesodermal layer.

My own sections also show that it arises on each side of the œsophagus as a groove lined by mesoderm (Plate X. Fig. 92, right). This canal, which is shown cut along its course in Plate IX. Fig. 82, *can. crc.*, is not wholly separated from the body cavity, but communicates with it below the brain. This communication occurs in the section below that shown in Figure 82, near the point *can. crc.* This ring canal at an earlier stage is shown in Figure 87. It has not yet been formed backwards nearly so far as the brain; anteriorly the section has traversed the tentacles under which it runs. The canal is also shown cut across in Figure 86 at the base of a tentacle, with whose lumen its cavity is directly continuous.

The formation of the tentacles is closely connected with that of the ring canal, from the upper wall of which they arise. Since the upper wall of the ring canal is two-layered, the tentacles are two-layered also. The outer layer of the tentacle is thus derived from the inner layer of the bud; the inner layer, on the contrary, from the outer layer of the bud. It would be hardly necessary to make this statement, which agrees both with early and the most recent observations, had not Barrois ('86, p. 75, Fig. 48) referred to and figured the tentacles as having been formed from the inner layer of the bud *only*.

My observations fully confirm Seeliger's ('90, p. 587) description of the manner of growth of the tentacles; that is, that the outer edge of the ring canal, together with its tentacles, moves downward and outward along the sides of the polypide, turning the axis of the tentacle from a nearly horizontal to a vertical position, and increasing the area of the kamptoderm. Thus in Figure 92 this process has progressed farther on the left side than it has on the right.

Nitsche ('71, p. 458) lays some stress upon the statement that the tentacles are not at first few in number, gradually becoming more numerous; on the contrary, he says, "Ich sah stets, beim ersten Auftreten von Tentakelanlagen, 16, 17, oder 18 Stück gleichtzeitig erscheinen." Seeliger ('90, p. 584) agrees with Nitsche in this respect; but Prouho ('90, p. 449) finds the conditions different in Flustrella. Here the tentacles "ne se développent pas simultanément sur tout son pourtour, mais apparaissent d'abord de chaque côté du plan de symétrie, puis se multiplient vers l'arrière." As I have shown, 14 of the 17 tentacles arise nearly simultaneously in Paludicella, for here there are few of them; and this is the case also in Escharella variabilis with its 17 tentacles.

As the tentacles of both Flustra and Bugula are few in number,[1] the statements may easily be considered to be correct for these genera. The tentacles of Flustrella hispida are much more numerous (30–35), and Prouho's statement may well be true for his form. In fact, my own observations on this species are fully in accord with those of Prouho. Figure 77 (Plate IX.) represents a young polypide of a Flustrella corm, viewed from the roof as an opaque object. Six tentacles were visible on each side of the bud, but the oral and anal parts of the corona were yet incomplete. The remaining nine or ten pairs of tentacles subsequently arise oralward and analward of these rudiments.

Much disagreement has prevailed concerning the number of layers involved in the *kamptoderm* of marine Gymnolæmata, in both the adult and the developmental stages. As in so many other cases, we owe to

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[1] Bugula avicularia has 14 or 15 tentacles, and Flustra (Membranipora) membranacea 20, according to Hincks ('80, pp. 76 and 140).

Nitsche ('71, pp. 431, 432) our first intimate knowledge of this organ. He believed it to consist in the adult of Flustra of a single cell layer, in which are imbedded (or applied?) longitudinal and circular muscle fibres. He believed the kamptoderm to be formed gemmigenetically only by the outer cell layer, the derivative of the mesoderm. Repiachoff ('75, pp. 138, 139) observed in Tendra (Membranipora) "die Doppelschichtigkeit der Tentakelscheide nicht nur bei den jungen Knospe sondern auch bei den ganz ausgewachsenen, offenbar schon längst functionirenden, in ihrem mittleren Theile ganz braunen 'Polypiden,'" and later ('76, p. 152) a similar two-layered condition of the kamptoderm (Tentakelscheide) in Membranipora and Lepralia. Ehlers ('76, p. 37) finds a single layer of cells in the kamptoderm of the adult Hypophorella (Ctenostome), which he believes is continuous with the endocyst of the body wall, and thus is ectodermal. He finds neither longitudinal nor circular muscle fibres. Haddon ('83, p. 517) believes the kamptoderm to be derived from both the inner and outer layer of the polypide bud. Vigelius ('84, pp. 33, 82) describes it as arising from the mesoderm only (Parenchymegewebe), and as being essentially one-layered, both longitudinal and circular muscles lying in this layer. Barrois ('86, p. 74) derives the kamptoderm from the mesodermal layer only. Ostroumoff ('86^a, p. 15) believes the kamptoderm to be two-layered and provided with muscles; it is in his opinion derived from both layers of the bud. Freese ('88, pp. 18, 19) studied only the adult of Membranipora. He admits the presence of muscle fibres, but believes the kamptoderm one-layered. Pergens ('89, p. 507) states only that in the Cheilostomes studied by him the tissue of the kamptoderm is composed "aus abgeplatteten Zellen, zwischen welchen Längs- und Ringmuskelfasern eingebettet sind." Prouho ('90, p. 451) states that in the primary polypide of Flustrella this organ is early differentiated, "et les deux couches de rudiment prennent part à sa formation." Finally, Seeliger ('90, p. 587): "Es kann danach keinem Zweifel unterliegen, dass die Tentakelscheide ektodermalen Ursprungs ist. . . . Das Mesoderm erscheint auf allen gelungenen Schnitten von der Tentakelscheide scharf abgesetzt."

It is my belief that throughout the group of marine Gymnolæmata, as in Paludicella and Phylactolæmata, the kamptoderm is derived from both of the two layers of the polypide bud, is provided with a strong system of longitudinal and a slight one of circular muscles, and contains in the adult two layers, or at least modified representatives of two layers. I have arrived at this conclusion from a careful study by sections of the following genera: Bugula, Lepralia, Escharella, Flustrella, Bowerbankia, and Crisia. The existence of two layers was easily demonstrated in all cases in the young polypide by cross sections of the "neck." The two layers are of nearly the same thickness, and distinctly separated from each other. The presence of two layers in the adult is more difficult to determine, but it was always indicated by the occasional presence of two nuclei lying side by side, and especially at the attachment to the diaphragm. The presence of muscles was demonstrated in all cases (except Bowerbankia, where my few sections did not show the proper region) upon tangential sections of the sheath. I may add, that the existence of muscles is wellnigh conclusive *a priori* evidence of the existence of the mesodermal layer, since nowhere else in Bryozoa, so far as I know, do muscles arise from any other layer. Prouho's evidence in support of his position is perfectly satisfactory to my mind, certainly more so than the negative evidence of Seeliger in support of his. In further support of my statements I may refer to the condition of the kamptoderm (*kmp'drm.*) in Figures 92 and 83, Plate X.

Nervous System. — Since Dumortier discovered, in 1835, a ganglion in Lophopus, there has been seen in marine as well as fresh water Bryozoa a body which has been considered, with greater or less certainty, to constitute the central nervous system. Overlooked by Farre, it was, I believe, first described for marine Gymnolæmata in 1845 by van Beneden, co-worker with Dumortier, for Laguncula (Farrella). Nevertheless, up to the present the evidence of its being a ganglion homologous with that of Phylactolæmata has not been satisfactory. The homology can be established only by determining its similar origin with the brain of Phylactolæmata; its function can be best established by showing the existence of ganglionic cells and fibres. I hope to have advanced our knowledge in both of these directions.

At about the time that the œsophagus and stomach have become confluent, one notices a papilla-like elevation of the floor of the atrio-pharyngeal cavity. This has been noticed by Korotneff ('74) in Paludicella, and by Nitsche ('71, p. 459) and Seeliger ('90, p. 586) in Cheilostomes. It has been called by them "Epistome," and compared with that of Endoprocta or Phylactolæmata. In my own opinion, it is merely a structure brought into prominence by the sinking down of the floor behind it to form the ganglion (Plate X. Fig. 86, *gn.*). This depression has been seen by Barrois ('86, pp. 74, 75) and Prouho ('90, p. 450), and rightly interpreted by them as probably destined to give rise to the central nervous system. That this is the correct interpretation is shown by later stages from different species, as Figures 89 and 83, in which we see the ganglion gradually assuming the position it has in the adult, on the anal side of the pharynx at the base of the anal tentacles.

A section across the pharynx in such a stage as Figure 83 is shown in Figure 87. A comparison with Figure 51 (Plate V.) of my Cristatella paper (Davenport, '90) will show a great similarity of conditions at about the same age, and can leave no doubt concerning the homology of the regions marked in both cases *lu. gm.*; or compare Taf. VIII. Fig. 100, *nh.*, of Braem's ('90) magnificent work. A section through a later stage is shown in Figure 82. The brain has already sent out circumœsophageal nerves, as in Paludicella. The central part of the ganglion does not stain; one sees only a granular mass, sometimes with signs of short fibres. In the cornua (*n'*) one occasionally sees very large clear nuclei with a single nucleolus, lying in the midst of a cell mass which is spindle-shaped and stains more deeply than adjacent cells. These remind one strongly of bipolar ganglionic cells, but fibres could not be traced far from their pointed ends. Series of sections of Flustrella parallel to Figure 82 show, as one passes below the level of the ganglion, a continuous band of cells extending down from it towards the cardiac valve and between the cell layer lining the œsophagus and the surrounding mesoderm. One is reminded of the exactly similar conditions in Paludicella (page 26), and of the "linienartige Zeichnung" seen by Nitsche ('71, p. 431) and Vigelius ('84, p. 42) in the same place in Flustra. These facts go to indicate the existence of a gastric nerve.

At about the time at which the ganglion arises, the cavities of the stomach and the œsophagus become confluent (Fig. 86 *œ.*). At this stage (somewhat earlier than Figure 86) the alimentary tract consists of a U-shaped tube of nearly uniform calibre, and without any indication of the cœcum. The tentacles lie in two parallel rows in the middle of the bud, the corona being incomplete both in front and behind, but less so oralwards than towards the anus (Fig. 77, *atr.*). In fact, while new tentacles are formed later towards the oral median line, they never appear behind the line *atr.* This hinder region has another fate. Its wall increases very greatly in area, diminishes correspondingly in thickness, and forms a large part of the kamptoderm lying behind the postoral tentacle in Figure 86. With this growth of the kamptoderm the anus is carried backwards, and farther and farther from the posterior ends of the rows of tentacles, immediately behind which it formerly lay.

As the kamptoderm grows in area, the polypide comes to lie in the proximal part of the zoœcium. *Pari passu* with this process occurs the *rotation of the oral tentacles,* as in Paludicella. The oral tentacles which at first lie perpendicular to the roof of the colony (Fig. 86) gradually come to lie parallel with it (Figs. 89 and 83). The œsophagus loses its elongated, laterally compressed form, and becomes circular, and the ganglion lies just below the mouth-opening. Not until now, in fact, can one speak of a mouth. It was not at all formed synchronously with the anus. To illustrate this process I have taken three different genera representing different stages. Similar stages could have been obtained from each genus. By using three genera, the similarities as well as the dissimilarities of the process are indicated. Among other things, the larger size of the polypide and shorter kamptoderm of the Ctenostome Flustrella (Fig. 89) is noticeable.

Lastly, the cœcum is formed as a wholly secondary differentiation of the alimentary tract. This arises in some species relatively earlier than in others; thus it is better developed in Figure 86 than in the later stage of Figure 83.

The lining cells of the alimentary tract now rapidly undergo the differentiations characteristic of the different regions. The most extreme modification takes place in the *pharynx*. In Cheilostomes the cells of this region gradually become vacuolated, until finally very little stainable protoplasma remains. The nucleus lies at the deep end of the cells. A very peculiar modification of the cell walls takes place, in that they become plainly perforated by holes through which the adjacent cells are in communication (Fig. 85). It is in a region similar to this that the cells become cuticularized in Bowerbankia to form the so-called gizzard. The pharyngeo-œsophageal region is also provided with a very powerful musculature of circular muscles (*mu.*, Figs. 85, 86).

Concerning the *origin of the muscles* I have made very few studies. The parieto-vaginal muscles seem to arise, as in Paludicella, from around the neck of the polypide, and the retractors from the oral end of the polypide bud (*mu. ret.*, Fig. 89).

The *neck of the polypide* sinks below the general level of the body wall by an infolding of the latter, as described for Paludicella, and the mass of columnar cells which passes down with it forms, I am confident, the *diaphragma* of Nitsche ('71, p. 432), which is thus exactly comparable with the mass of cells around the atrial opening of Paludicella in Figure 45, *of. atr.* (Plate V.). According to this view, then, the diaphragma is not placed at about the middle of the kamptoderm, but at its proximal end, and all that lies between it and the outer body wall — the non-evaginable portion — has been formed in the elongated neck, exactly as the non-evaginable portion is formed in Phylactolæmata (see

Davenport, '90, Plate IX. Fig. 77, Plate XI. Fig. 98) and Paludicella (Plate V. Figs. 50 and 45).

As my purpose is not so much to present a complete organogeny of Bryozoa as to show the method of origin of the bud and the fate of the layers, I have had to desist from carrying on my studies further in the organography, and have left many interesting and important questions unsolved; such, for instance, as the development and structure of avicularia, the presence of an excretory system, and the degenerative processes which occur with regularity in the polypides.

3. Regeneration of the Polypide.

I have been led to study the regeneration of the polypide because Ostroumoff seems to believe that in regenerating buds the digestive epithelium of the stomach is derived from an extraneous source, — the brown body. Thus he says ('86^a, p. 340) the brown body appears as a cœcal appendage of the young digestive tube. "C'est sur ce dernier [tube digestif] qu'on trouve un groupe de cellules affectant la forme d'un bonnet et se réunissant très tôt à l'angle proximal du rudiment ectodermique. A mesure que les cellules du bonnet, ainsi que la masse brune, sont employées à la formation de la portion moyenne du tube digestif, ces dernières se débarrassent de leur contenu," etc.

The external phenomena of regeneration are well known. In the Membranipora stock, for instance, one sees polypides being produced at the margin, and one finds them older and older as one passes backwards, until finally they are seen to be wholly degenerate, and to be replaced by young polypides. Thus, in passing backward along a single row of individuals in a Membranipora stock about 18 mm. long, I have seen this process of regeneration recurring four times. In Alcyonidiun, too, one finds an apparently regularly recurring degeneration and regeneration of polypides. In the mat-like Cheilostomata the regenerating polypide (Plate VIII. Fig. 71, *pyd. rgn.*) is always found at one place, — namely, on the operculum, — that is, proximal of the opercular opening.[1] In Flustrella it is found in a similar position on the dorsal body wall, proximal of the cuticularized introverted portion. My studies have been chiefly made on the Cheilostomata. Figure 91 (Plate X.) represents an early stage in the formation of a regenerating polypide. Here, as in the marginal polypides, there is a typical invagination involving the two layers of the body wall (*i.*, *ex.*). Owing to the reagent, the body wall is shrunken from its contact with the operculum (*op.*).

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[1] Haddon ('83, pp. 522, 523) has found the regenerating polypide arising from the same place in Flustra membranacea and in Eucratea, and Ostroumoff ('86^a, p 339) in Cheilostomes in general.

If one inquires what has been the histological conditions of this region antecedent to this stage, one must look to younger adjacent and marginal zoœcia, since they reproduce these conditions. I will again call attention to Figure 88, which represents a cross section of the body wall through the region of attachment of the kamptoderm of a young polypide of about the stage of Figure 83. This, then, represents the neck of the polypide, and it is from about this region that the operculum and finally the regenerating polypides will arise. The cells are columnar, and stain deeply about the nuclei, and both cell layers are well developed. Elsewhere in this same individual the body wall is composed of smaller, flatter cells, and two layers are not easily distinguished. The region of the future operculum possesses at an early stage some of the largest, most columnar cells of the body wall. The cells of this region do not, however, retain their peculiarly large size throughout life, but in the adult we find the same region occupied by a flat epithelium, nearly as thin as the epithelium shown in Figure 90. Meanwhile the epithelium of the rest of the body wall has become still more attenuated. The difference between the body wall of the operculum and that of adjacent regions is best shown by the greater abundance of nuclei under the opercular region when the stained stock is looked at *in toto* from the roof (Plate VIII. Fig. 71). The regions of the future opercula are seen, in young zoœcia (Fig. 71, *4*, *6*), to be patches of densely packed nuclei. The opercula of older zoœcia show a slight preponderance of nuclei, and thus indicate more numerous cells. It is from such a region, then, that the young regenerating polypide arises.

As in the case of the marginal polypides, so here, the lips of the invagination pocket close and become fused to form the neck of the polypide (Plate X. Fig. 84). The later stages of the development of the regenerating polypides seem to be the same as those of the marginal buds. Figures 74 and 89 are, indeed, regenerating polypides. I cannot find any evidence that the alimentary tract, or any part of it, is formed in regenerating buds by a method differing in any essential particular from that in marginal buds.

It is well known, however, that the degenerated polypide which forms a "brown body" in the old zoœcium eventually disappears. Haddon ('83, p. 519) maintains that in the developing regenerated polypide "the walls of the stomach, or, more strictly, that portion of the stomach which forms the gastric cœcum, grow round and envelop the brown body, so that the brown body passes as a whole into the alimentary tract of the young Flustra." It seems to me that the burden of proof of such a remarkable occurrence lies with him who asserts its existence, and certainly sufficient evidence is not presented by Haddon.

To settle this question in my own mind, I cut a series of thin sections through a part of a stock of Escharella (which in budding shows a practical identity with Flustra), in which all stages of regenerating polypides were to be found. From complete series, at critical ages, I utterly failed to find any indication of the inclusion *in toto* of the brown mass by the polypide. But I found the alimentary tract of the polypides usually applied to the brown body (*pyd. dgn.*), as shown in Figure 92. At this stage the degenerated mass is surrounded by spindle-shaped cells, and just within these by a homogeneous or lamellated sheath. At later stages the elements of the degenerated mass were seen to be more loosely associated. The cells of the alimentary tract at the same time appear highly granular, and a granular coagulum often partly fills the alimentary tract. Before the new polypide is ready to expand itself, the brown body as such has often wholly disappeared. Just as my sections leave no chance for the brown body to be included *en masse* by the alimentary tract, so too do they yield no evidence of the addition to the latter of new cells from this degenerate mass, as Ostroumoff, in the sentence quoted above, implies.

The interesting facts of degeneration in Bryozoa deserve a more careful study than I have been able to give them. We are quite ignorant of the physiological significance of the regularly recurring degeneration and regeneration in certain Bryozoan colonies. Ostroumoff ('86^a, p. 339) has offered an interesting hypothesis, to the effect that the degeneration of the polypides, the remains of which are taken into the stomach of the regenerated polypide and the undigested portion of which is cast out with the fæces, is a method of excretion, made necessary to these animals from lack of urinary tubules.

IV. Origin of the Gemmiparous Tissue in Phylactolæmata.

After having found that in Paludicella and the marine Bryozoa, as in Phylactolæmata, the growth of the colony takes place at the margin or tips, and that it is here primarily that buds originate, and after having thus found that throughout the group all of the organs of the polypide are derived from two layers, of which the inner gives rise to organs so dissimilar in origin as the central nervous system and the alimentary tract usually are, it becomes a matter of no little importance to solve the two problems, what is the origin of these growing regions, and what that of the two layers. Through the works of Barrois ('86), Ostroumoff ('87), Vigelius ('88), and especially Prouho ('90), on the metamorphosis of the larva and formation of the first polypide of Gymnolæmata we are fairly well acquainted with the facts in this group; but a careful study has not heretofore been made of the Phylactolæmata with reference to the points mentioned above. Korotneff ('89) and Jullien ('90) have published quite extensive papers on the ontogeny of Phylactolæmata, which describe too incompletely the stages which should reveal the required facts.

In order to throw a little light on these questions, I undertook the study of the embryology of two species of Phylactolæmata. But before beginning the account of what I have found, it is necessary to remind the reader of some facts concerning the origin of the polypides in the adult colonies. For our knowledge of these we are chiefly indebted to Braem ('90, pp. 18–32) ; it has also been my privilege to confirm many of them.

The details of the budding process are slightly different in Plumatella and Cristatella. In the latter genus the body wall becomes highly modified as it grows older by the formation of secreted masses which nearly fill most of the ectodermal cells. In Plumatella, on the contrary, the ectodermal cells retain, for the most part, a more primitive, unmodified condition. Here, moreover, by a rapid growth at the neck of the polypides, the individuals are carried to considerable distances from one another, whereas in Cristatella there is a less rapid growth resulting in a compact stock.

In Plumatella, the whole of the embryonic tissue from which any bud arises does not go to the formation of a polypide, but a part of it remains as the neck of the polypide, and gives rise by cell proliferation to the body wall and the *Anlage* of a new bud. Thus the *Anlage* of each bud is part of that of a preceding bud. The question remains yet unsolved, Whence came the *Anlage* of the first polypide? Since the embryonic tissue of the inner layer of the bud, which seems to take the most active part in the formation of the bud, gives rise to both the lining of the alimentary tract and the wall of the brain, it becomes an exceedingly interesting question, From what germ layer is this inner bud layer derived?

In Cristatella, as in Plumatella, not all of the embryonic tissue from which any bud arises goes to form that bud; but some of it is, apparently, passed along under the highly metamorphosed cells of the ectoderm, again to divide itself, one part going to form a new polypide, the other to form the *Anlagen* of new buds. In Cristatella, this embryonic mass of cells of the inner layer of the bud seems to be to a considerable extent independent of the highly metamorphosed ectoderm, and to form at places a sort of third layer, lying below the true ectoderm and above the muscularis with the cœlomic epithelium. Here, too, while it is easy to see buds arise from preceding buds in the adult colony, we cannot consider our question answered until we have discovered the origin of the cells from which, as from a stolon, the *Anlagen* of polypides successively arise.

I desire to say that I have avoided giving a full account of the ontogeny of these species, both because it is not directly required for the solution of the problems in hand, and because we are promised studies in this field by Braem.

The eggs of Phylactolæmata arise, as has long been affirmed, from the cœlomic epithelium of the body wall. The evidence of this is conclusive, for one often sees in a single section various stages in the development of the eggs. (Plate XI. Fig. 93, *ov'*.) It is also to be observed that they do not arise indiscriminately from any region of the body wall, but always close to the neck of a polypide. Sooner or later these eggs, surrounded it may be by a few follicular cells, are enclosed in an oœcium, and here undergo their development up to the stage of a young stock, possessing perhaps a dozen immature polypides. In the figures on Plates XI. and XII. the oœcium (*oœ.*) has been usually drawn, but in Figures 100 and 104 it has been omitted. As a result of cleavage, a blastula is formed, and from one pole of this — *the pole nearest to the neck of the oœcium* — cells are given off which move into the blastocœl (Figs. 94, 98) and finally come to line the cavity. It is important to observe that in the earliest stage of this process found there were four inner cells, of which two are represented in the section (Fig. 94, *ms'drm.* + *en'drm.*). Thus the two layers of the adult body wall are established. Up to this stage the conditions are practically the same in Cristatella and Plumatella. From now on, they are somewhat different in the two genera.

The first difference to be noticed is in the oœcium itself. In Cristatella the cells composing this rapidly become a pavement epithelium (Fig. 97); in Plumatella, on the contrary, the cells of the oœcium remain columnar (Fig. 99). The neck of the oœcium also differs in the two cases. In Cristatella it is long, thick, and filled with a dense mass of large cells (Figs. 95, *cev. oœ.*, and 101 *, 102 *). In Plumatella (Fig. 99) it is very short.

The second difference concerns the embryo itself, and is connected with the formation of the first polypide. In Plumatella (Fig. 99) the first indication of the formation of the first polypide occurs at or very near the neck of the oœcium, or, since the ingression of cells into the blastocœl took place at the pole of the blastula nearest the neck, we may say near to the pole at which ingression occurred. The cells of the outer layer (*i.*) are elongated and contain large ellipsoidal nuclei which are often pressed close together. All of the cells of the larva stain more deeply at this pole than elsewhere, and those of the inner layer rather more deeply than those of the outer. The nuclei are also very large, those of the outer layer being possibly more prominent than those of the inner; but the difference is not so marked as in the drawing, where too the nucleoli of the inner layer are represented relatively too small. Even at this stage one finds in another section of the same embryo the beginning of a second polypide, whose position is indicated at *. This second polypide is indicated merely by a considerably thickened inner larval layer, and a very slightly thickened outer one. The two polypides are thus seen to be wholly independent of each other. The first invagination further advanced is seen in cross section of the whole larva in Figure 96. The entire outer layer would seem at first sight to be involved in this invagination; but even in this figure there are seen one or two nuclei which lie under the oœcium at the place of invagination. I believe that they will not be involved in it, for at a very little later stage (Fig. 104) one finds a layer of cells lying over the invaginated bud, which I believe are destined to form the ectoderm of the body wall at this place.

Later stages in the development of the larva in this species are not shown. The bud follows, I am confident, the same steps that are pursued by the bud in the adult colony. A placenta-like connection of the larva with the oœcium, which was first described by Korotneff ('87, p. 194), begins at about this stage, and continues until two well formed polypides are present. This "gürtelformige Placenta" begins to form in about the middle of the young embryo, and the elongated cell of the outer layer of the larva, in contact with the oœcium shown on the left of Figure 99 below the *, is, I believe, the first indication of it. The oœcium and larva both continue to increase in size, and the walls of the former become thinner with their increase in area.

The attachment of the oœcium to the body wall of the mother stock always remains small, as in Figure 99, and the embryo, in my experience, does not come in contact with it.

The formation of the first polypide in *Cristatella* is preceded by another process. Just as in the adult colony the inner layer of the polypide does not arise by invagination of the ectoderm, but from the stolonic cells lying at the base of the ectoderm (see Davenport, '90, pp. 108, 109, Figs. 4 and 15), so too in the embryo. The first process then must be the formation of the stolonic cells. Figure 101 shows at the point marked *sto.* (which is at the pole of the embryo whence the inner-layer cells originated) that certain of the cells of the ectoderm appear to be arching over a disk, containing about six cells in section, and thus coming in contact with the cylinder of cells (*) which projects from the neck of the oœcium. By a continuation of this process, the central disk of cells gradually comes to lie below the general level of the ectoderm, and to be cut off from contact with the neck of the oœcium (Fig. 97, *sto.*). The position of the stolonic mass with reference to the neck of the polypide in this last figure must be considered abnormal; it is at any rate exceptional, as it lies at one side of the neck of the oœcium, which does not, therefore, appear in this section. The next later stage which I have found is shown in Figure 102. The stolonic mass seen lying beneath the ectoderm in Figure 97 has here already given rise to a young polypide (*i., ex.*), and its area is increasing in all directions by cell division (*sto.*). The beginning of a second polypide is indicated on the right at *sto.* The ectoderm is seen lying above this stolonic mass, and closely applied to the neck of the oœcium (*).

Neither at this nor at any subsequent stage have I been able to detect in Cristatella any "gürtelformige Placenta" such as exists in Plumatella. I am therefore of opinion that the process of nutrition, which is effected in Plumatella from the oœcium through its placenta, is effected in the Cristatella larva by its attachment to the neck of the oœcium. I am pleased to see that Jullien ('90, pp. 13, 14) has also reached this conclusion in a paper which he has had the kindness to send me. At a later stage, the embryo, or young colony, seems to become detached from its intimate association with the neck of the oœcium, as we see in Figures 95 and 103.

Figure 103 represents a stage in which there are two well developed buds, both shown in the section. There is, in addition, on another section, one less developed. The stolon is seen passing oralward of these two primary polypides, or rather the primary and secondary one. Moreover, as the series of sections shows, the stolon does not exist merely in this section, but it is a disk which is cut here in one of its diameters. A separation of the stolonic mass has occurred between the two oldest polypides, so that the ectoderm is here in contact with the cœlomic epithelium, just as is the case between buds in the adult stock. As the colony increases, the inner and outer margins of the stolonic tissue continue to extend farther outward, and this tissue forms at first a broad ring of ever increasing diameter. Later, as the area of the stock increases, the ring becomes broken, so that, instead of growing along an infinite number of radii, its growth is confined to a few, as in the adult colony.

I will defer a discussion of the significance of these facts to the general part of this paper.

B. GENERAL CONSIDERATIONS.

I. Laws of Budding.

Carefully conducted studies on stock building have generally revealed, just as these on Bryozoa have shown, a law in budding. This law in budding results in the formation of a stock the interrelation of whose individuals is a determinate one. I now propose to offer an hypothesis to account for the existence of these laws, and then to show how facts of budding in Bryozoa and other groups can be explained by means of it.

And first of all I must acknowledge that this hypothesis, although perhaps here first formulated, really depends upon observations and deductions made long ago on this group, first by Hatschek, who from 1877 has maintained that individuals do not arise independently of one another, and secondly and mostly to Braem, who in '88 (pp. 505, 506) declared of Phylactolæmata "dass in dem Stock keine Knospe entsteht, die nicht auf das embryonale, d. h. den specifischen Leistungen der Körperwand noch nicht angepasste Zellmaterial einer älteren Knospenanlage zurückgienge und dass somit in der ersten Knospe des keimenden Statoblasten sämmtliche Knospen des künftigen Stockes implicite enthalten sind." Not less is the following hypothesis indebted to the ideas of Roux and Fraisse, and to Nussbaum, who has said ('87, p. 293): "Ein lebendes Wesen ist somit als Ganzes oder in seinen Theilen soweit individualisirt und vergänglich, als die Gewebebildung und die Theilung der Arbeit vorgeschritten ist; das Ueberdauern der Einzelexistenz, die Theilbarkeit auf geschlechtlichem oder ungeschlechtlichem Wege, spontan oder künstlich bedingt, ist an das Vorhandensein undifferenzirter Zellen gebunden und ist um so grösser, je weiter im Organismus diese Zellen verbreitet sind"; and, finally, to the idea which is implied in the conclusions of Nussbaum ('80, pp. 106–113) and Weismann, that germplasma does not find its origin in the parent individuals, but is merely borne by them in its unbroken passage from generation to generation.

This hypothesis is simply that *there is in every stock of Bryozoa a mass of indifferent cell material which is derived directly from indifferent cells of the larva or embryo, and whose function is to form the organs of the various individuals, including the polypides.* This indifferent cell material lies in the body wall, principally at the growing tip or margin of the stock. By its growth and differentiation it gives rise to the body wall, muscles, etc., and at intervals it leaves behind, as a portion detached from itself, a mass of indifferent cells, which is capable of forming a polypide, or of becoming a new centre of growth, or of both. Which of these possibilities will be fulfilled, where and when these masses of indifferent cells will be left behind, depends upon the necessities of the species, and the variations in these respects give rise to the peculiar characters of the different stocks.

This hypothesis differs from that of Braem in that the pre-existence of a *Knospenanlage* assumed by Braem is, according to my view, a non-essential feature in the formation of the colony; the pre-existence of an indifferent cell mass, which does not itself constitute buds, but may give rise to masses which can, is the only essential feature.

As a first application of this hypothesis I refer the reader to the conditions of stock formation in *Paludicella*, already described. We find at the tip of the colony a mass of large proliferating cells, which I regard as histologically undifferentiated. These cells give rise to the body wall, — the cystid, — and at intervals leave behind three masses of cells, which I regard, from the fact that they retain their cuboid condition, as well as from their ultimate fate, as indifferent or embryonic. The median mass of each of these gives rise to a polypide, and to one only. The lateral masses form centres of growth similar to the one from which they were derived.

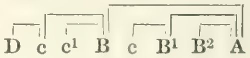
In order to reproduce the arrangement of individuals in the stock resulting from this manner of budding, we may make use of some graphic method of representation, as Smitt ('65^a, pp. 139, 140) did long ago, and as Allman ('70), Semper ('77, pp. 67–78), Chun ('88, pp. 1167–1180), Braem ('90, pp. 33 and 44), Ehlers ('90, p. 9), and others, have since done. I shall represent the mass of indifferent cells by an asterisk, and individuals (according to Chun's nomenclature) by the use of the large and small letters of the Roman alphabet, and, finally, by Greek letters. The typical stock of *Paludicella* might then be graphically represented thus (cf. Plate I. Figs. 2 and 2^a) : —

```
                                                *
                                              * c *
                                              *   *
                                            * α b α *
                               *              *   *
                             * b *          * *   * *
                             *   *        * β α a α β *
                  *        * α a α *        * *   * *
        *       * a *      *     *
(1)   ✲ D         C           B               A
        *       * a *      *     *
                  *        * α a α *        * *   * *
                             *   *        * β α a α β *
                             * b *          * *   * *
                               *              *   *
                                            * α b α *
                                              *   *
                                              * c *
                                                *
```

Here the letters indicate polypides or their *Anlagen*, and the asterisks indifferent tissue. The individuals represented by capital letters may be called primary individuals; they may be said to belong to the primary series, and to have been derived from the primary indifferent mass. The individuals represented by small Roman letters will then be secondary individuals, belonging to the secondary series and arising from secondary masses, etc. It is to be observed that this indifferent tissue is here found only at the tips of branches or *Anlage* of such. No asterisks are found adjacent to the adult polypides A, B, C, etc., which have given rise to lateral branches, and these have therefore no power of producing new parts of the colony. The asterisks must not be regarded as having been descended from the letters which they adjoin, but from the terminal asterisks only; that is to say, in Paludicella embryonic tissue has originated from terminal embryonic tissue, and not from indifferent tissue left remaining alongside of the polypides.

Conditions differing in an interesting manner from these were found by Braem ('90, pp. 18–32) and myself (Davenport, '90, pp. 103–106) in Phylactolæmata. In *Plumatella* Braem has shown in the clearest manner how some of the embryonic tissue around a polypide at the proximal end of a nascent branch is carried away to the oral side of the "mother polypide," and lays the foundations of another polypide. In like manner the embryonic tissue around the "mother polypide" may give rise to one or several additional embryonic masses. He has also (pp. 29–32) shown in the most convincing way that each mass, particularly in the case of secondary buds, consists of two parts, of which one goes to form the polypide; the other contributes to the further growth of the common cystid and the formation of new embryonic masses. Since here every embryonic mass is in intimate relation with a polypide, and since the polypides arise nearly in one plane, only secondarily moving out from it, the relation of individuals may be expressed by a formula occupying a single line. Braem has thus expressed it: —

(2)



According to the system adopted for Paludicella, this may be given thus: —

(3) $*\alpha \quad *a \quad *b \quad *A \quad *a \quad *B \quad *C$ ❋

or, more developed, thus: —

(4) $*\alpha_1 \quad *\alpha \quad *\beta \quad *a \quad *\alpha \quad *b \quad *c \quad *A \qquad *\alpha \quad *a \quad *b \quad *B \quad *a * C \quad *D$ ❋

in both of which the right hand asterisk (❋) takes the place of the A at the right of Braem's diagram. These symbols denote that we have a mass of indifferent tissue connected with each polypide, or the *Anlage* of such; and this indifferent mass, as well as the adjacent polypide, was derived from some other indifferent mass. Thus the masses connected with A, B, C, D are to be regarded as having been cut off from the embryonic mass at the extreme right; and each of these secondarily gives rise to the polypide buds a, b, etc., and their embryonic tissue. Thus we have to do with centrifugal budding only.

In *Cristatella* the conditions are essentially similar to those in Plumatella, the chief difference being that usually only two polypides with their embryonic masses arise from each polypide. This condition may be represented by the formula: —

(5) $*\alpha_1 \quad *a \quad *\beta \quad *a \quad *\alpha \quad *b \quad [*]A \quad *\alpha \quad *a \quad *b \quad [*]B$ [❋]

in which the embryonic masses originally attached to A, B, etc., are bracketed to indicate that they are normally no longer active in giving rise to new polypides. As a matter of fact, the secondary rows often make a greater or less angle with the primary ones, and as a result lateral branches are formed. Taking this character into account, the Cristatella formula might be written : —

$$
\begin{array}{ccccccc}
 & & & & & & \ast \\
 & & & & \ast & & \mathrm{b} \\
 & & & \ast\alpha_1 \;\text{—} & \alpha & & \vert \\
 & & & & \vert & & [\ast] \\
 & & \ast\beta & \text{—} & \ast\mathrm{a} & \text{—} & \mathrm{A} \\
 & & & & & & \vert \\
\ast\mathrm{b} & \text{—} & [\ast]\mathrm{B} & & \text{—} & & [\ast] \\
 & & \vert & & & & \\
\ast\alpha & \text{—} & \mathrm{a} & & & & \\
 & & \ast & & & &
\end{array}
\tag{6}
$$

This representation indicates the fact that the first formed buds (A, a, α, etc.) are lateral ones ; the second, median (Davenport, '90, p. 106). Intermediate stages between the condition in Plumatella, in which an indefinite number of polypides and gemmiparous masses can be budded off from pre-existing gemmiparous masses, and the condition in Cristatella, in which only two such arise, occur apparently in some species of Plumatella, in which, as Braem ('90, p. 31) has shown, few polypides are produced from any gemmiparous mass, and all but two of these generally do not develop. In the young corms of Cristatella, on the other hand, more than two polypides may thus arise.

Other *Ctenostomata* show a regularity in the budding process similar to that of Paludicella, and exhibit instructive variations upon it.

Victorella, an interesting Ctenostome occurring in slightly brackish water, and first described by Kent ('70) in 1870, possesses, according to the pregnant observations of Kraepelin ('87, pp. 75, 76, 154–157), a stolon-like tube, from which at intervals polypide-bearing " cylindrical cells " arise. Kraepelin ('87, pp. 155–159) has shown it to be in the highest degree probable that the protrusion of the body wall in the neck region of the polypide of Paludicella is the homologue of the " cylindrical cells " of Victorella, and that the remainder of the zoœcia of Paludicella is homologous with the " stolon " of Victorella. While in Victorella the cylindrical cell is developed to such an extent that the retracted polypide is still included within it, and the stolon remains of small calibre, in Paludicella, owing to its shortening, the retracted polypide must seek refuge in the stolon, whose diameter is consequently increased to receive it. Evidence for this is found in the stolon-like nature of the youngest zoœcia of a hatching winter bud of Paludicella Ehrenbergii, and in the elongated cylindrical cell of the adult Paludicella Mülleri, Kraepelin, which must be considered a form intermediate between P. Ehrenbergii and Victorella.

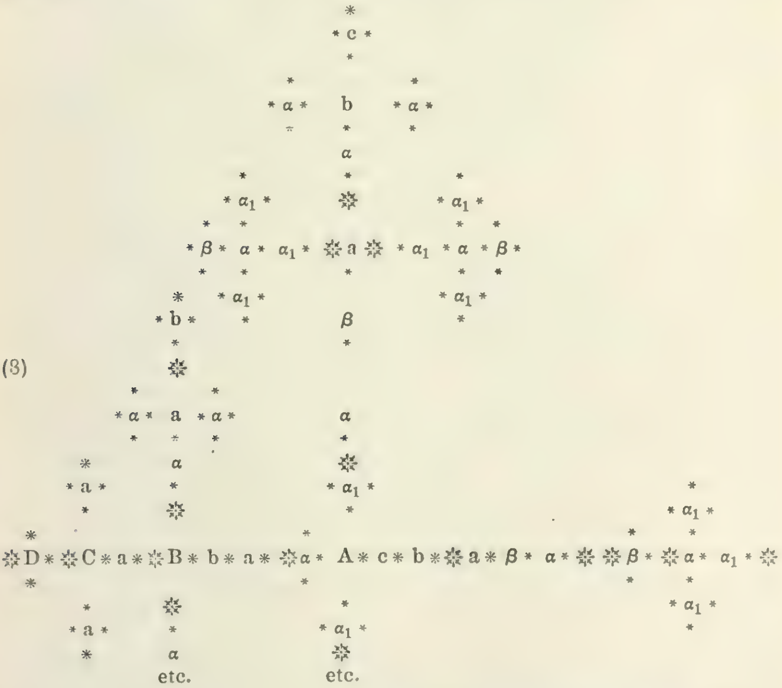
The architecture of the Victorella and Paludicella stocks is, then, similar, in that they both consist of a row of individuals successively formed at a stolonic tip. The resemblance is heightened by the fact that, as in Paludicella, so also in Victorella, a pair of lateral buds is given off from each zoœcium to form lateral branches (Kraepelin, '87, p. 157). As in Paludicella, so also in Victorella, communication plates, *Rosettenplatten*, arise early to separate the zoœcia from each other. But Victorella differs from Paludicella in this, that while in the latter the neck of the polypide does not become the centre of origin of new buds, in the former it does, just as is the case in Plumatella (Kraepelin, '87, Plate III. Fig. 75) ; that is to say, there are laid down from the tip of the branch three masses of bud-producing tissue, besides that which goes to form the polypides of the primary branch. The graphic representation of this species will therefore be more complicated than that of Paludicella, and has this form : —

```
                                                         *
                                                       * c *
                                                         *
                                                    *         *
                                                  * α *  b  * α *
                                                    *    *    *
                            *                  *    *         *     *
                          * b *              * β *  α *  a  * α   * β *
                            *                  *    *    *    *     *
               *       *        *
             * a *   * α *  a * α *                      α
               *       *    *   *                        *
        *
(7) ✲ D * C * a *    B *   b *   a * α *     A *  c * b * α *  a * β *  α *
        *
               *       *    *   *                        *
             * a *   * α *  a * α *                      α
               *       *        *
                            *                  *    *    *    *     *
                          * b *              * β *  α *  a  * α   * β *
                            *                  *    *         *     *
                                                    *    *    *
                                                  * α *  b  * α *
                                                    *         *
                                                         *
                                                       * c *
                                                         *
```

Compare with (1), page 73, and (4), page 74.

From around each individual of the series A, B, C, etc., which has been derived from the tissue of the stolon tip, there arise series of lateral and of median buds. From around each of the lateral buds, in like manner, both lateral and median buds of a higher order arise. But from each of the median buds only median buds arise. These median buds, are not, however, all of the same kind. The one first produced (a ∗, of Formula 7, ❊ of Form. 8) differs from all formed after it (b ∗, c ∗, d ∗, etc.) in this, that it bears no polypide, but forms the tip of a stolon from which both median and lateral buds arise (β, a, near extreme right of Form. 8). From the second and all succeeding median buds (a b, c, etc., Form. 8), there arise only median buds of a still higher order. Of the latter, the first, as before, produces no polypide, but becomes the tip of a stolon giving rise to both median and lateral buds ; the others give rise to only median buds of a still higher order, and so on. Our former formula assumed that all median buds were alike, and all incapable of giving rise to lateral individuals. Their dissimilarity introduces a complication, so that the species must be represented by some such formula as this[1]: —

(8)



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[1] It must be borne in mind that such a graphic representation as this, while it agrees with the descriptions and figures of Kraepelin and Hincks ('80, Plate 79) so

in which the heavy asterisks represent the budding tips of the stock, which give rise to new individuals (tips of the stolons), and α_1, β_1, etc. indicate individuals of the fourth order. The lighter asterisks indicate, as before, points of proliferation from which new buds may arise.

It seems highly probable that Victorella finds near allies in Mimosella and other genera of the Stolonifera.

In *Hypophorella expansa,* according to Ehlers ('76, pp. 5–9) and Joyeux-Laffuie ('88, pp. 137–139), the stolon is composed (as in Victorella), of a number of internodes, each separated from the other by communication plates, and bearing on the distal end typically a feeding zoöid (Nährthier) and a lateral stolon. It seems to me that the jointed condition of the stolon is reasonably accounted for in the same way as that of Victorella, by supposing that each internode, together with its zoœcium, is comparable with the whole indvidual of Paludicella. The "feeding zoöids" of Hypophorella will then be comparable with the *Cylinderzelle* of Victorella. Two facts are opposed to this view: first, the polypide is not formed primarily in the stolon, coming only secondarily to lie in the *Cylinderzelle* as in Victorella; and, secondly, there is a *Rosettenplatte* in Hypophorella between the feeding zoöid and the stolon, while none exists in Victorella. But upon this assumption one can best account for the fact that the stolon is composed of as many joints as there are feeding zoöids, — a condition which appears to occur in only a few other genera, and these closely allied to Victorella. Thus, in Cylindrœcium pusillum and C. dilatatum of Hincks we have two species which may be considered to represent two possible intermediate stages between Victorella and Hypophorella, not only on account of the jointed stolon, but also on account of the enlarged distal end of the joint, which is eminently characteristic of the allies of Victorella. The first objection, that the polypide is not developed in the stolon, but first arises in the well formed zoœcium of the feeding zoöid, might result from the increased importance of the zoœcium over the *Cylinderzelle.* The formation of the plate between the zoœcium and the stolon might be accounted for by the physiological need of such an organ resulting from the increased importance of the zoœcium (cf. p. 40). Such plates exist, in fact, between the primary median individuals, and those secondary median ones in Victorella which are budded from the *Cylinderzelle.* This hypothesis

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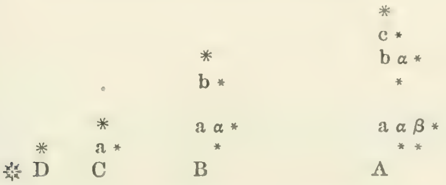
far as they go, may not fit the conditions in all parts of the colony. Moreover, it is to a certain degree idealized, i. e. subjective, for even in the figure of Kraepelin ('87, Fig. 75) one of the individuals of the series a, b, c, etc. has given rise to no stolon as its first bud.

is further supported by the fact that, as a stolon may arise from the *Cylinderzelle* of Victorella, so in Hypophorella such a condition is not uncommon, although hardly typical. In accordance with this hypothesis the formula for Hypophorella might be given thus: —

(9)



$$\begin{array}{cccc} & & & * \\ & & & \mathrm{c}\ * \\ & & * & \mathrm{b}\ \alpha\ * \\ & \cdot & \mathrm{b}\ * & * \\ & * & \mathrm{a}\ \alpha\ * & \mathrm{a}\ \alpha\ \beta\ * \\ * & \mathrm{a}\ * & * & *\ * \\ \circledast\ \mathrm{D} & \mathrm{C} & \mathrm{B} & \mathrm{A} \end{array}$$

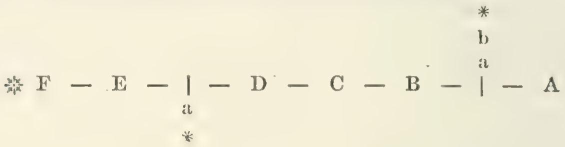
Ehlers ('76, pp. 127, 128), in founding the group of Stolonifera, classified the different methods of arrangement of the individuals in the colony as follows: —

I. Many polypides (*Nährthiere*) on the single joints of the stolon (*Stengelgliedern*).
  1. On the entire length of the joints.
    (a.) Arranged in two rows.
    (b.) Arranged in a spiral.
    (c.) Arranged in one row.
  2. At the ends of the joints.
    (a.) In rows.
    (b.) Massed.

II. Only one polypide *Nährthier* on a joint of the stolon.
  1. Polypide lateral, near it one or many stolonic joints (Hypophorella).
  2. Polypide terminal.

In the present state of our knowledge, it is very difficult to say how the types of budding shown in those Stolonifera which possess more than one *Nährthier* on a joint of the stolon are related to, or are to be connected with, the types of Paludicella, Victorella, Hypophorella, or other genera possessing only one *Nährthier* to a joint. This could doubtless be determined, however, by studying the early stages in the development of the stocks. Taking them as they are, however, we find a very simple condition in the stocks of Class I., in which the *Nährthiere* are arranged in a single row, as in *Vesicularia spinosa* (cf. Hincks, '80, Plate 73, Figs. 3–7). The tip of the stolon consists, as I have myself observed in allied species, of somewhat cubical cells of variable thickness, and it is from this tip that the *Anlagen* of the individuals arise. Lateral branches occasionally replace a *Nährthier*, and the latter seems never to produce secondary individuals. The formula of the stock might be written : —

(10)



$$\begin{array}{ccccccccccccccc}
 & & & & & & & & & & & & \ast & & \\
 & & & & & & & & & & & & b & & \\
 & & & & & & & & & & & & a & & \\
\circledast\,F & - & E & - & | & - & D & - & C & - & B & - & | & - & A \\
 & & & & a & & & & & & & & & & \\
 & & & & \ast & & & & & & & & & &
\end{array}$$

In *Bowerbankia pustulosa* we have two rows of individuals produced side by side from near the end of the stolon. This condition would be represented by

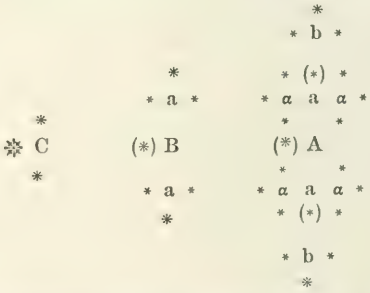
$$(11)\qquad \begin{array}{ccccc}
\circledast & \ast\,D & \ast\,C & \ast\,B & \ast\,A \\
\circledast & \ast\,D & \ast\,C & \ast\,B & \ast\,A
\end{array}$$

provided the individuals of this primary series possess the power of giving rise occasionally to secondary buds, as seems certainly to be the case in some members of this genus which I have seen. The spiral arrangement of some colonies is striking ; it is of evident advantage to the stock, but its cause in these cases is wholly unknown.

In every one of these cases, and, in fact, in all of those figured by Hincks, which belong to the Stolonifera, there is no trace of dichotomy. Throughout we have to do with linear series, which give rise to lateral branches.

Turning now from the Stolonifera to the other grand division of Ctenostomata, the *Alcyoniidæ,* we find the same prevalence of a law in budding. In its typical expression it may be written as follows : —

(12)



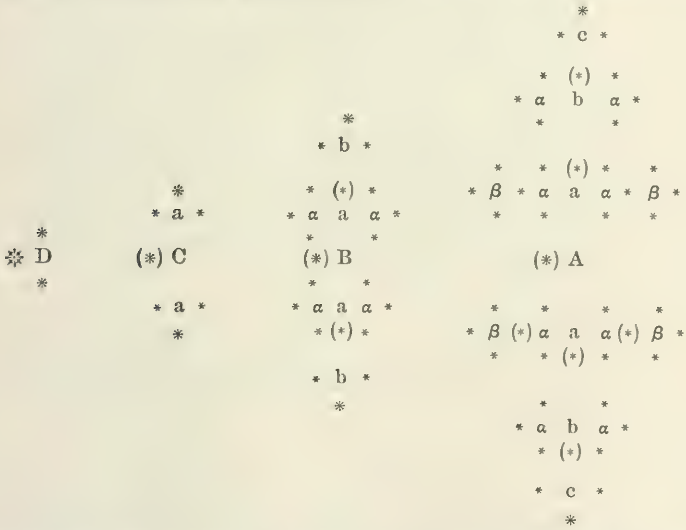
$$\begin{array}{cccccccccc}
 & & & & & & & \ast & & \\
 & & & & & & \ast & b & \ast & \\
 & & & \ast & & & \ast & (\ast) & \ast & \\
 & & \ast & a & \ast & \ast & \alpha & a & \alpha & \ast \\
 & \ast & & & & & \ast & & \ast & \\
\circledast & C & & (\ast)\,B & & & & (\ast)\,A & & \\
 & \ast & & & & & \ast & & \ast & \\
 & & \ast & a & \ast & \ast & \alpha & a & \alpha & \ast \\
 & & & \ast & & & \ast & (\ast) & \ast & \\
 & & & & & & \ast & b & \ast & \\
 & & & & & & & \ast & &
\end{array}$$

Although secondary median individuals are not habitually formed, yet, owing to the capacity of regeneration possessed by individuals A, B, C, etc., an asterisk is affixed in parentheses to show the probable persistence of embryonic tissue. Of the lateral series one or both may fail to be developed.

It might be difficult to determine whether in this group we have to do with dichotomy, did not the tips of the margins at times reveal the fact that there is no division of the ancestral series, but that a new one is added at the side of an ancestral one (Plate VIII. Fig. 69), where of the marginal individuals 4 is clearly median (ancestral) and 3 is lateral, 13 median and 12 lateral, etc. (see page 49).

The members of the group of *Cyclostomata* seem to be closely related, and the method of budding is so similar throughout the group that it seems fair to interpret the more compact Tubuliporidæ from the Crisiadæ. In *Crisia*, as we have seen, individuals are placed in rows, from which at intervals lateral rows are given off to the right or left. One may say that typically these are given off from each individual to both the right and the left, although in some cases, as in Figure 65^a, lateral branches are typically given off alternately to the right and left, and are often aborted. Perhaps the most general formula of all for Cyclostomes should be that of two lateral branches from each individual, one or both of which may remain undeveloped. Such a formula I believe to be also the typical one for *Bugula* and its allies, and for the *Flustrina* and *Escharina*. It would be written thus: —

(13)



in which the parenthesized asterisks indicate the presence of regenerative tissue. This is identical with (12) and similar to (1).

Braem ('90, pp. 130–133) has already called attention to the difference between Phylactolæmata and Gymnolæmata in the *orientation of the* *polypide.* In Phylactolæmata the oral aspect of the polypide is turned towards the margin of the corm or the tip of the branching stock; in Gymnolæmata, on the contrary, the anal aspect is turned in that direction. This difference is a very striking and constant one. It is correlated with another difference in the law of budding of the stock, which will become evident upon comparing Formulas (4) and (5) on page 74, of Phylactolæmata, with Formulas (1) on page 73 and (7) to (13). In all of these the margin or tip of the stock is at the left, the centre at the right. In the formulæ of Phylactolæmata the budding is *centrifugal*, new individuals being produced from the embryonic masses towards the margin; in the formulæ of Gymnolæmata budding is *centripetal*, new individuals being produced from the embryonic masses towards the centre. *In both Phylactolæmata and Gymnolæmata the anal aspect is turned towards the gemmiferous region.*

Braem calls attention to one other difference, namely, that, in the case of the retracted polypide, in Paludicella the rectum lies next the attached surface of the stock; in Phylactolæmata, the œsophagus. A mechanical cause of this is suggested when this statement is put in other words: the polypide in its retracted position is stored in both Phylactolæmata and Gymnolæmata proximad of the atrial opening; i. e. away from the tip or margin, and towards the centre of the stock. May not this be explained, in part at least, as an adaptation to room?

I will here add four examples of regular budding taken from other groups of animals, to illustrate the general applicability of this method of representation. The first of these is that of the Siphonophore *Halistemma* whose formula has been worked out by Chun ('88, p. 1169), and expanded and illustrated by Korschelt und Heider in their recent textbook (p. 39). It runs as follows: —

(14) D c b a C d c b a B e d c b α a γ β α A

According to my interpretation of the case, this formula might be written (15): —

❊D ❊c ∗b ∗a ∗C ❊d ∗c ∗b ∗a ∗B ❊ ∗e ∗d ∗c ∗b ∗α ∗a ∗γ ∗β ∗α ∗A,

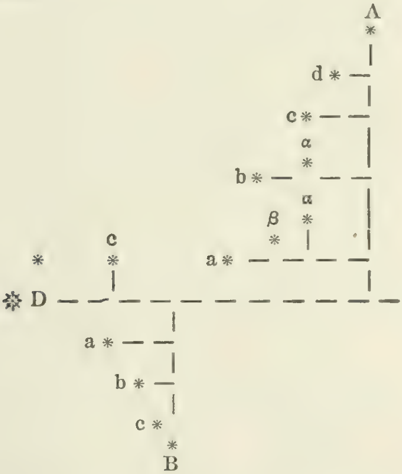
in which the ❊ behind B has been derived from the embryonic mass at A, that behind C from B., etc. The ❊'s represent embryonic masses from which a, b, c, etc. are derived.

If we assume that the terminal individual (A) has not been derived from the primary embryonic mass, at the extreme left, but has had its origin in the embryo, the formula would have to be written somewhat differently; namely, thus (16): —

❊ C❊ c∗ b∗ a∗ B❊ d∗ c∗ b∗ a∗ A❊ e∗ d∗ c∗ b∗ α∗ a∗ γ∗ β∗ α∗ [A]

In a species of *Pennaria*, common on our coast, which is probably Pennaria tiarella, McCready,[1] I have noticed the presence of a similar law of budding. The whole stock lies in one plane, the lateral branches arising alternately from the right and left of a central stock, like the barbs of a feather. These lateral branches give rise to a series of secondary ones, which are all placed on the same (axial) side of the branch. Each branch, of whatever degree, originates as a bud bearing a polyp. From the elongating stalk of this terminal polyp, buds arise, — the beginnings of branches of the next higher order. The stock may be represented by the following formula: —

(17)



Expressed in a linear series, this formula may be written: —

(18) ❊ D∗ C∗ B∗ c∗ b∗ a∗ A∗ d∗ c∗ b∗ α∗ a∗ β∗ α∗

which is identical in form with the second formula (16) given for Halistemma.

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[1] This species is figured by Leidy ('55, Plate 10, Figs. 1–5) and Verrill ('73, Plate XXXVII. Fig. 277). An allied species, P. gibbosa, is figured by Louis Agassiz in the "Contributions" (Vol. III., Plate XV. Fig. 1). In describing P. Carolinii, Weismann (Entstehung der Sexualzellen, p. 122) says that the lateral hydranths do not possess the capacity of giving rise to new lateral hydranth-buds (of a higher order). But, as indicated above, P. tiarella seems to do this regularly. Leidy's and Verrill's figures show the same thing.

Lastly, this formula may be applied to certain cases of fission, as in *fresh water Annelids.* As is well known, the fissiparous process is preceded by the formation of the so-called budding zones (Knospungszone). These arise in *Ctenodrilus*, according to Kennel ('82, pp. 403, 404), between two dissepiments in the middle of a metamere, and new ones are continually formed behind the others as the animal grows in length by cell proliferation at the tail end. The budding zones are, according to Kennel, regions composed of embryonic cells. I think it probable that this embryonic tissue has been derived from the embryonic tissue of the anal end of the animal. There are as many budding zones produced as there are new metameres added by the anal growth, and since the budding zones are intrasegmental, each zoöid consists of four parts; viz. (naming them from anterior to posterior end) of the posterior half of the preceding budding zone, of the posterior half of the metamere in which the budding zone arose, of the anterior part of the next following metamere, and, finally, of the anterior part of the following budding zone. Zoöids then are made up of parts of two adjacent metameres, and the middle of each zoöid is intersegmental. The zoöid has progressed little beyond the state of possessing two (half) metameres at the time it becomes free. New metameres must become formed by caudal growth. The animal is, then, according to my conception of the significance of the process, derived chiefly from these budding zones. Evidently, the law of production of new individuals (or new budding zones) is a simple one, and may be written, in accordance with my nomenclature,

(19) ❊ E (*) * D (*) * C (*) * B (*) * A

in which A, B, C, etc. represent successive individuals (adjacent halves of two metameres), and the asterisks, as before, embryonic tissue. The two adjacent asterisks together represent the budding zone, of which the posterior half (parenthesized) proves itself the least active.

The conditions given by Semper ('77, pp. 69, 77) for *Chætogaster* (and Nais) are much more complicated, but may be expressed by the use of a formula constructed upon the same plan. Chætogaster differs from Ctenodrilus in this: that young budding zones, and eventually young individuals, are produced between older ones, instead of always at the anal end; and the new zoöids often acquire several metameres before becoming free. It seems to me probable that, as in Ctenodrilus, the budding zones are derived ultimately from the anal zone; but here, in contradistinction to Ctenodrilus, new budding zones may secondarily arise from other budding zones produced earlier, thus giving rise to the phenomena of young individuals interpolated between older ones. Representing, then, individuals by the budding zones from which they have arisen, we may convert the following formula of Semper into one based on our own nomenclature :

$$az. - \overbrace{3+0}^{E} - 0 \quad \overbrace{4+0}^{D} - \overbrace{1+0}^{H} - 0 \quad \overbrace{4+1}^{B} - \overbrace{1+0}^{G} - 0 \quad \overbrace{4+0}^{C} - \overbrace{2+0}^{F} - 0 \quad \overbrace{4+1}^{A}$$

in which the succession of generations of zoöids is

. . . 5, 4, 8, 2, 7, 3, 6, 1.

In the above formula A, B, C, etc. represent zoöids; the numerals below the letters, the number of metameres of which each is composed; 0, an incomplete metamere about to be derived from a budding zone; *az.*, the anal zone. Written in accordance with my conception of the facts, this formula would read :

(20) ❊ D (∗) ∗ C (∗) ∗ a (∗) ∗ B (∗) ∗ b (∗) ∗ a (∗) ∗ a′ (∗) ∗ A,

which somewhat resembles Formula (15) of Halistemma, and signifies that two embryonic masses are left behind by the anal zone, of which the one anterior to the zoöids proper (represented by letters) goes merely to form the head parts, and is represented parenthesized. The second is caudad the zoöid, and may form a secondary "anal zone" giving rise to new zoöids. From one zoöid two or more anal zones may take their origin. Thus, from the embryonic mass caudad of A there have arisen that caudad of b, which has given rise to b (∗) ∗ a (∗), and that caudad of a′, which has given rise to a′ (∗).[1]

The most general formula given on page 81 undergoes many modifications in the different groups, but in the midst of these modifications certain laws are to be discerned, to some of which I have already called attention. I will now proceed to a discussion of the significance of these laws.

The *quincunx* arrangement of individuals, which is so noticeable in the phytoid stocks of Bugula, and in creeping corms like Lepralia or Cristatella, may be explained as affording additional strength on the one hand, and as a device for saving space on the other.

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[1] From a study of surface views of many specimens of Autolytus collected at Newport during June, 1891, I am convinced that the sexual individuals are produced by proliferation of cells in the metamere XIII. or XIV. of "parent form," — the last which remains behind after breaking off of sexual form. Representing the proliferating metamere by (❊), we may write the budding formula of Autolytus thus:

(20^{a}) ❊ E (∗) D (∗) C (∗) B (∗) A (∗)

in which the parenthesized asterisks indicate the proliferating, but not gemmiferating anal metameres of the sexual form. (Cf. A. Agassiz, '63, pp. 397–400.)

The absence of true dichotomy, which I have sought to show characterizes the budding of Bryozoa, is interesting as seeming to indicate the fundamental similarity of the process of budding in Paludicella to that found elsewhere. The tip of the branch does not divide equally in the first nor in the other instances, but constantly maintains its precedence, giving off parts of itself to form lateral branches. These parts may grow out at right angles to the primary branch, as in Paludicella, but generally they grow forward nearly parallel to it, as in most marine Gymnolæmata.

In Bugula (Plate VII. Fig. 64^a) branches are always given off *toward the axils,* and therefore an ancestral branch gives off all lateral branches from one side and the successive orders of branches are given off alternately to the right and left. In Crisia, on the contrary, branches are given off *abaxially,* and they are given off not from one side only, but alternately to the right and left. In both cases the two facts are mutually dependent. The first case gives rise to a stock in which the branching tends as greatly as possible towards compactness and the formation of a closely built stock ; the second case gives rise to a diffuse and loosely built stock (cf. Figs. 64, 65, and 64^a, 65^a). In the second case there is a maximum space to each individual ; in the first, a maximum *economy* of space.

The rule that lateral buds on two closely related branches tend to arise in the same generation is one that, as has been shown, is more or less apparent in some cases, but is easily obscured by other rules. May not the tendency be due to the same causes that produce the synchronism of division in related cells of a cleaving egg ?

That lateral buds should occur in *Bugula flabellata* on the outermost rows only is not surprising when we reflect that there is abundant room on the margin, whereas the inner individuals are hemmed in from lateral expansion by the pressure of adjacent rows. This is very marked in certain repent colonies, as, for instance, occasionally in Membranipora (Plate VIII. Fig. 70). Here the intermediate branches 6, 7, 8, and 9 have produced no lateral buds for many generations, while almost every individual of the marginal rows has given rise to a lateral branch. It is merely a result of the same cause, it seems to me, that lateral budding occurs more frequently in *Bugula turrita* at the margins of fans than elsewhere. Here there is room to spread.

The rule (5) that ancestral rows contain fewer *generations* of individuals than lateral ones may perhaps receive a partial explanation from the further fact (rule 6) that of the two rows starting from any axil the ancestral branch will give rise to a greater *total number* of individuals than the lateral one will in the same time. We should expect a less rapid forward growth if the lateral growth is extremely vigorous. One might also say that the intermediate rows had grown abnormally in length, since that is the direction in which there is most room.

The reason why the ancestral branches in Bugula give rise to the greater total number of individuals is, to my mind, because they are marginal. In Crisia it is the lateral branches which are the most prolific, and for the same reason.

The existence of the 7th rule in mat-like species is a mechanical necessity; in the phytoid species, like Bugula and Crisia, it must be accounted for on another ground; namely, on the relations of food supply to demand, — on the deterrent effects of overcrowding. And this, to my mind, is the key to the significance of the 4th, 5th, 6th, and 7th rules. The form of the stock is determined by the same law which has determined the form of the individuals, — the struggle for existence and the survival of the fittest, — the fittest in the present case being those which are most advantageously placed with reference to food supply. Abundant food supply has made possible the rapid production of lateral individuals at the margin, and less abundant food supply has retarded such production in the middle. Therefore has lateral budding occurred more rapidly at the margin; therefore has the number of individuals produced at the margin been greatest; therefore have the median rows grown *in length only* with great rapidity; therefore has the distance between adjacent rows of individuals in phytoid stocks remained constant.

Many observations on different groups of animals agree in demonstrating a relation between rapidity of the budding or fission process and food supply. Thus Zoja ('90, pp. 25–27) has shown for Hydra, and Zacharias ('86, p. 274) and von Wagner ('90, p. 360) for Turbellarians, that abundant food supply results in an acceleration of the processes of non-sexual reproduction, and Braem ('90, p. 24) has shown that budding in Cristatella proceeds less actively during the late fall. This diminution in activity has been attributed by Braem to diminished temperature; but we know also that this period is one of scarcity of the small fresh water organisms upon which the fresh water Bryozoa live (cf. Parker, '90, pp. 597–600), and this fact also must be considered as having an important influence in this case.

II. Relation of the Observations on Budding in Bryozoa to the Germ Layer Theory.

No question in Bryozoan morphology has been more thoroughly discussed than that of the part played by the germ layers in the production of the polypide, and upon none has there been less agreement. Nitsche first boldly opened the question, and concluded that we have in this process a fatal objection to the idea of the homology of the germ layers, in so far as their homology depends upon a similarity of fate throughout the Metazoa. A single layer, the invaginated ectoderm, gives rise to the outer covering of the tentacles, to the pharynx, and to the brain, — structures elsewhere considered as ectodermal, — and also to the lining of the alimentary tract, elsewhere universally accounted entodermal. In view of these facts, "sind die Keimblätter," concludes Nitsche ('75, p. 398), "keineswegs mit einer besonderen histologischen Prädisposition ausgestattete Zellschichten, sondern lediglich die flächenhaft ausgebreiteten Elemente, aus denen die den Metazoenkörper zusammensetzenden, ineinander geschachtelten Röhren sich bilden." Prouho, although recognizing the facts to be as stated by Nitsche, has not discussed the theoretical bearing of the question. Seeliger ('89^a, p. 204) finds in the budding process of Endoprocta a shortening and confusion of the embryonic process. "Wie die gesammte Knospenentwicklung verkürzt ist, erscheinen auch die beiden Processe der Einstülpung durch welche im Embryo zuerst Entodermkanal, dann Atrium sich bilden, in einen zusammengezogen." In another place (Seeliger, '90, p. 595) the budding process is considered as an "immer sich erneuerende Gastrulationsvorgang." Braem ('90, p. 116) regards the inner layer of the bud as entoderm, and the process of its formation as one of gastrulation. In a preliminary notice published last February (Davenport, '91, p. 279) I suggested that the embryonic tissue from which the inner layer of the polypide arises is to be regarded as "neither ectoderm nor entoderm, but as still indifferent, and capable of giving rise to either." A few weeks ago I saw for the first time the paper of Oka ('90), in which he offers (p. 145) *a priori* a similar suggestion concerning the significance of the embryonic tissue from which the inner layer of the polypides arises. I am pleased to find that our ideas, thus independently arrived at, are so fully in agreement. My idea of the relation of the germ layers to the layers of the polypide bud chiefly grew out of my studies on the embryology of Phylactolæmata as described in earlier pages.

As there are two layers to the bud, the question of the part taken by the germ layers in the polypide bud may be subdivided into two: What is the significance of the outer layer of the bud? and, What is the significance of the inner?

The *outer layer of the bud* is derived from the cœlomic epithelium. The views of those who have studied the formation of this inner layer of the cystid in Phylactolæmata may be classed in two categories: (1) those in which it is regarded as entoderm, and the process of its formation as gastrulation; and (2) those in which it is regarded as mesoderm. To the former class belong the views of Reinhard ('80, p. 208), Korotneff ('89, p. 403), and Jullien ('90, p. 19); to the latter, those of Kraepelin ('86, p. 601) and Braem ('90, p. 116), and in this class the views of Barrois ('86, p. 68) and Haddon ('83, p. 543), founded on *a priori* considerations, must be placed.

It seems to me that, since, as Barrois has demonstrated, there is a great similarity between the Phylactolæmatous and Gymnolæmatous larvæ, and especially since the former show evident signs of degeneration, we are bound to study the phenomena they exhibit in the light of our knowledge of the ontogeny of Gymnolæmata.

But first it is necessary to give reasons for believing that the larva of Phylactolæmata is to be regarded as homologous with that of Gymnolæmata; and to do this I will first name the points of similarity in the two larvæ, and then try to show that the differences which exist are not sufficient to invalidate the attempt to establish a homology. And, first of all, it may be said that, since the adult Phylactolæmata and Gymnolæmata are strikingly similar to each other, and since no one doubts their close relationship, we should expect *a priori* that their larvæ would be homologous, especially since the larvæ of Gymnolæmata are admitted to belong to the trochosphere type, of whose ancient origin there can be little doubt. In the second place, the very existence of a larval stage in Phylactolæmata is indicative of its inheritance from an earlier condition, for two reasons: (*a*) because in general fresh-water life tends to eliminate larval stages from species which have inherited them from marine ancestors, and tends little to form them *de novo* (Hydra, fresh-water Turbellarians, Rotifera, Oligochæta, Hirudinea, Astacus, and fresh-water Mollusca); and (*b*) because, specifically, the early stages of development of Phylactolæmata are passed within a uterus-like sac, from which the embryo is released only when a colony is already well established. In the third place, the Phylactolæmatous larva possesses, in common with all Gymnolæmatous larvæ, the following characteristics. The primary polypides arise in both at a pole, and this pole is in both a prominent disk, surrounded by a circular fold, — the so-called mantle fold, — from which it is separated by a circular groove, — the so-called mantle cavity. This organ has a similar origin and fate in the two groups, as shown by Barrois.

The following points of difference, however, must be recognized. First, the absence of a definite ciliated ring, *couronne* (Barrois), of an internal sac, and of a pyriform organ. But, as Barrois ('86, p. 67) has shown, these are absent, or at least (Ostroumoff, '87, pp. 182, 183) little developed, in Cyclostomatous Bryozoa. The ciliated ring and pyriform organ are doubtless organs connected with a free locomotive larval life, which is greatly abbreviated in Phylactolæmata. A second difference exists in the fact that, while most Gymnolæmatous larvæ possess either, rarely, (1) a functional alimentary tract, or (2) a mass of loose tissue lying inside of the ectoderm, the Phylactolæmata possess (3) a central space lined by an epithelium placed next to the ectoderm. However great the difference between the first and third conditions mentioned above, it is to a large extent bridged over by the widespread existence of the second. In some Cyclostomes, moreover, a similar condition to that in Phylactolæmata seems to exist. Compare Metschnikoff ('82, p. 310, Taf. XX. Fig. 62). Lastly, the origin of two primary polypides, instead of one, at the aboral pole, upon which Barrois has laid some stress, cannot be considered a very strong objection to the homology, because in reality the two polypides do not arise at the same time even in Plumatella, and in Cristatella this difference is still more pronounced. In fact, it is not the formation of *two polypides* which requires explanation, but that of a young *stock* before hatching.

There remains, therefore, to my mind, no serious objection to regarding the larvæ of Phylactolæmata and Gymnolæmata as having been derived from some common ancestral larva, possessing, of course, more points of resemblance to the Gymnolæmatous than to the Phylactolæmatous type; and therefore it is perfectly justifiable to interpret the latter by aid of the former.

Admitting the larvæ to be homologous, we should expect the process of *gastrulation* to be comparable throughout Ectoprocta. As a matter of fact, we do find a great similarity in the earliest stages. Thus, the first indication of the inner layer is the ingression of four cells at one pole, which by multiplication give rise to a layer of cells lying inside of the ectoderm.[1] It is to the comparative study of the fate of this inner layer in the different Ectoproct larvæ that we must look for an explanation of the layer in the specific case of the Phylactolæmata.

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[1] This has been shown for Membranipora (Tendra) by Repiachoff ('78, pp. 416–420); for Alcyonidium polyoum by Harmer ('87, pp. 445, 446); for Bugula by Vigelius ('86, p. 519); and for Cristatella in the present paper (page 68).

For the purposes of this study, it is desirable to begin with species in which there has been a minimum amount of degeneration. Such are Membranipora (Cyphonautes), Alcyonidium, and Flustrella, to which we must now turn our attention.

The studies of Repiachoff on Membranipora lead up to a stage in which the entoderm lies as a solid mass inside the ectoderm, and is separated from it at all points. Neither the origin of the mesoderm nor the formation of stomodæum or proctodæum was observed at this time. As for the fully formed Cyphonautes, it is certain, as I can confirm from personal observation, that there is a well developed functional alimentary tract, and that it is provided with a well developed muscular system, including cross-striped muscle fibres. There is, therefore, every reason for believing that typical entoderm and mesoderm have been formed in it.

In Alcyonidium (polyoum), Harmer ('87, p. 445) has shown that after gastrulation a great mass of cells occupies the former blastocœl. This, in the author's opinion, represents entoderm and mesoderm. The young larva possesses a mouth, an œsophagus, and a large stomach, but never an anus. No evidence is presented that the oral pole corresponds with the pole of ingression.

Flustrella, which is nearly related to the last species, possesses in its young larval stages a pocket, which Prouho ('90, pp. 424–426) has shown to represent the anterior part of the alimentary tract, directly comparable with that of Alcyonidium polyoum, but less developed. Muscle fibres and an epithelial lining of the entoderm and ectoderm exist to indicate the presence of mesodermal tissue.

These three genera, Membranipora, Alcyonidium, and Flustrella, are the only Ectoprocta in whose larvæ the presence of an alimentary tract has as yet been demonstrated.

In Bugula, a very careful study of which was made by Vigelius ('86 and '88), one finds after gastrulation and cell multiplication a mass of cells filling the whole interior of the larval body, at first appearing as an epithelium surrounding a central space, but later without arrangement and often showing signs of degenerescence. No definite separate mesoderm could be found, and at no time was any trace of an alimentary tract to be seen. Vigelius calls the mass derived from the four entodermal cells *Füllgewebe*, and he believes it to correspond morphologically to both "hypoblast and mesoblast." It is to be noted, however, as a point of considerable importance, that in his figures of the metamorphosing larva Vigelius ('88, Taf. XIX. Fig. 6) represents this tissue as having almost entirely disappeared; that which remains giving rise to the mesodermal lining — the outer layer of the bud — of the developing polypide.

There can be no doubt that the so-called oral pole of the Bugula larva corresponds to the mouth-bearing pole of Alcyonidium, but does it correspond to the pole of ingression of entoderm? This question has not been answered by Vigelius. The existence of homopolar stages like that represented in his ('86) Figure 25, Taf. XXVI., makes it very difficult to establish this doubtful point.

The formation of the inner layer of Cyclostomes has been studied by Barrois ('82, p. 141). He says: "Dès les premiers stades les sphères vitellines glissent les unes sur les autres de manière à former une espèce de gastrula par épibolie et l'on ne tarde pas à rencontrer des stades d'un volume extrêmement exigu et déjà composés d'une couche exodermique et d'une masse endodermique libre dans son intérieur. La masse endodermique s'atrophie rapidement et l'on arrive à une petite blastula qui succède non pas à un stade composé de cellules radiaires dans lequel se forme une cavité centrale, mais qui est issu, au contraire, d'une vraie gastrula née par épibolie dans les premiers stades de la segmentation et dans laquelle la masse endodermique est déjà disparue." I have quoted Barrois thus at length, since his description will show forcibly at least one thing, that the fate of the cells which by ingression had entered the blastocœl is quite different from that of those in Bugula, where a great *Füllgewebe* is formed. Ostroumoff ('87, p. 183), however, has shown that the inner layer of the Cyclostome larva does not disappear, but comes to line the ectoderm as a very thin layer. In the adult larva, however, we find the contents of the ectodermal sac "filled with mesenchymatous cells, which are commingled with yolk granules and globules of albumen." It is these cells that produce the very considerable mesodermal layer of the first polypide, which arises in the metamorphosis of the larva. Here, as elsewhere, an apparently homopolar stage intervenes between gastrulation and the formation of larval organs, making orientation difficult.

Thus, passing from Cyphonautes, through Alcyonidium and Flustrella, Bugula, and finally Cyclostomes, we have a series in all of which the inner germ layer is derived from one pole by ingression or by 'epiboly," and in which there is a gradual reduction of the functional entoderm until it seems, in Cyclostomes, to be lost, and a gradual transformation of the mesoderm from a cell mass nearly filling the larva, and producing muscles and a lining to the body wall and alimentary tract, to a single thin cell layer lying next to the ectoderm, or to mesenchymatous cells extending through the cœlom.

This same series may be said, also, to be one in which there is a gradual decline in the complexity of larval organs. These find their maximum development in the bivalve Cyphonautes and Flustrella, and the complicated and beautiful Alcyonidium larva. They find their minimum development in the Cyclostomes, whose larvæ, instead of a girdle of flagella, possess merely an undifferentiated clothing of cilia, are reduced to a cylindrical or ellipsoidal form, lack the pyriform organ of other species, and in some cases possess only the rudiment of the internal sac.

If we were to imagine still another term at the degraded end of the series, it would be a form in which the four inner-layer cells that arise by ingression at one pole of the larva should give rise to little or absolutely no entoderm, in which the mesoderm should come to form an inner lining to the ectoderm, and in which the internal sac should be entirely absent. It is just these conditions which are fulfilled by the Phylactolæmatous larva.

Of all these changes, the loss of the entoderm is the most striking. What can be said in explanation of it? I would suggest this hypothesis: that *the entoderm of the Bryozoan larva has become rudimentary through loss of the alimentary function.*

In direct support of this hypothesis I have little experimental evidence to offer. One observation, however, which I made last summer, seems to favor this conclusion strongly. This is that larval life is of considerable duration in Cyphonautes, which possesses a functional alimentary tract, but is very brief in Bugula, in which no alimentary tract arises. As is well known, Cyphonautes occurs in enormous numbers in the "tow" at certain seasons of the year, and this is alone evidence of a considerable length of life. I have taken Cyphonautes thus obtained from the tow and have kept them for three or four days, at the end of which time they died, or had settled to the bottom of the glass vessel to undergo their metamorphosis. In fact, from several hundred Cyphonautes which I collected, not more than half a dozen completed their full metamorphosis, the others apparently succumbing to unfavorable conditions.[1]

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[1] Just as the manuscript of this paper is going to the printer, after long delay caused by an accident necessitating the re-engraving of the plates, I find that Dr. Prouho read last summer ('90), before the Association Française pour l'Avancement de la Science, a preliminary communication on the development of Cyphonautes. This is published in the printed report of the proceedings of that association. The

The *Bugula* larvæ, on the contrary, I have never found in the tow, but they swarm out from stocks gathered in the morning and placed in a glass vessel; and I can confirm Nitsche's ('69, p. 9) observation that they settle and begin their metamorphosis within "a few hours" after hatching. One rarely or never finds these larvæ succumbing to the unfavorable conditions of the aquarium before metamorphosing. From these observations I conclude that the Bugula larva has a very much shorter life than Cyphonautes. Now, since the larva, owing to its shortened life, has no need of functional entoderm, and since entoderm can be of use to the larva only, no part of it going over into the tissues of the primary polypide of the stock (except as food material), functional entoderm is not developed. In other genera, its rudiments have become less and less important in the ontogeny, and, finally, in Phylactolæmata are wholly lost.

That the entoderm should reach its last stage of degeneration in *Phylactolœmata* is easily understood when we consider that the larval period is passed in a closed oœcium, from the wall or neck of which it receives nourishment *as a parasite does.* Moreover, by the delay in the period of hatching, as well as by precocious development of polypides, one at least of the latter is usually functional in the just hatched stock, for there is sometimes found at least one polypide in the newly hatched larva, which is partly extruded, and therefore capable of feeding, and thus of supplying the whole stock with nutriment. Of what advantage to a species could be the development of a functional larval entoderm, which should go to form no part of its adult tissue, provided the larva was contained in a uterus during its early stages, and was provided with the adult digestive organs in a functional condition before leaving the uterus?

Those who maintain that the inner layer is to be regarded as entoderm, and are still unwilling to place the Bryozoa among the Cœlenterata, must account for the absence of mesoderm. Korotneff ('89, p. 400) finds degenerating cells in the blastocœl before this is wholly obliterated by the extension of the inner layer. These he seems to regard as degenerate mesoderm. According to his view, then, the entoderm gives rise to the muscularis, — for this arises from the inner larval layer, according

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author does not there state whether stomodæum and proctodæum are formed on the blastoporic side of the larva. He accounts for the existence of an alimentary tract in Cyphonautes by the fact that it undergoes its development disconnected with the parent, while almost all other Bryozoa pass their early stages in the parent or some protecting zoöid (oœcium, ovisac, ovicell).

to Braem's ('90, Taf. VII. Fig. 89 *mb.*) observations, which I can abundantly confirm, — and to the cœlomic epithelium of the adult stock. In the few series of sections of the proper stage which I possess, I have not found with certainty the degenerating cells of which Korotneff speaks; but even if they regularly occur, I should be inclined to regard them as the degenerated entoderm, the mesoderm persisting to give rise to the muscular tissue and the cœlomic epithelium.

From a consideration of these facts, — that the larvæ are homologous and the process of gastrulation is comparable throughout the Ectoprocta, that in the least modified larvæ both functional entoderm and mesoderm are produced by that gastrulation, that one of these two germ layers has become rudimentary in Phylactolæmata, that it is highly probable that the entoderm has disappeared from loss of function, and that the layer which persists gives rise to the musculature, sexual cells, and cœlomic epithelium, — I conclude that *the inner layer of the Phylactolæmatous larva, and therefore the outer layer of the bud, is mesoderm.*

If we accept the point of view of Kleinenberg ('86, pp. 1–19) and admit the existence in general of only two layers, ectoderm and entoderm, a clearer conception of the modification undergone by the Phylactolæmatous larva may be gained. We may divide the entoderm arising in Bryozoa into two parts; viz. (1) that which gives rise to the lining of the midgut, as in Cyphonautes, and (2) all the rest of the inner layer. Now, since no midgut is formed in the Phylactolæmatous larva, part (1) of the entoderm has ceased to be differentiated; all which remains, then, is part (2); but this is equivalent to "mesoderm" in the sense in which I have employed it, and therefore I am justified in saying that "mesoderm" only is produced.

The question has now to be answered, What is the significance of the *inner layer of the bud?* Two different answers have been given to this question. It has been maintained, on the one hand, that it is to be regarded as ectoderm; on the other, as entoderm. There are serious difficulties in the way of accepting the first view, — so serious, in fact, that few authors have maintained it, although at first glance it seems to be required by the facts. Although we have not yet sufficient grounds for declaring that organs formed by budding must be built up from the same germ layers as corresponding larval ones, — although we may admit that gemmigenesis recapitulates phylogeny and corresponds with ontogeny only in an imperfect and confused way, — still, from the experience gained by tracing the development of hundreds of animals from the most widely separated groups of the animal kingdom, the idea that a functional alimentary tract is ever wholly derived from differentiated ectoderm will not be accepted by most embryologists without conclusive evidence.

The second view is that the formation of the inner layer of the bud is a process of gastrulation, giving rise to entoderm, and that the so-called "gastrulation" of the sexual ontogeny of Phylactolæmata is to be regarded as a precocious ingression of mesoderm only.

Two considerations are opposed to this view. In Membranipora there is a gastrulation which gives rise to the entoderm and mesoderm of the larva; and since the gastrulation of Phylactolæmata is similar, these elements must be potentially present here also. The "gastrulation" in Bryozoa is a normal one; if there is any entoderm in the body wall giving rise to the inner layer of the bud, it must have been entoderm which failed to become invaginated. But what, in the second place, is to be gained by assuming that the inner layer of the bud is formed from entoderm? Here is as great a difficulty as before, since the nervous system originates from this layer. It has been maintained in many cases that the nervous system arises from *mesoderm*, and Seeliger ('89, p. 602) believes that it is formed from that layer in the non-sexual reproduction of some Tunicates; but I know of no good evidence of its origin in any of the Triploblastica from *entoderm*.

Before going on to state my conception of the significance of the inner polypide layer, I desire to call attention to the conditions in the region at which it is first formed. I have shown above (page 69) that the primary polypide or polypides arise from the pole of ingression in Phylactolæmata, and that therefore in this group the aboral pole (in the sense of Barrois) corresponds to the pole of ingression. As I understand Barrois, he means by oral pole merely the pole which in Cyphonautes, for instance, bears the mouth, — the pole also by which the larva attaches itself. Braem ('90, p. 123, foot-note), however, interprets "oral side" in Barrois's sense to mean in the last instance the place at which gastrulation takes place. Perhaps Barrois does somewhere state such to be the significance of his term (I have not found the place), but in that case I can only say that, to my mind, he has not produced sufficient evidence to prove that the oral pole of the larva of Gymnolæmata is the same as the pole of ingression in the gastrula; nor, in my opinion, has any other investigator done so. Nearly all species studied have a stage early in their development when their poles are very similar, and orientation certainly would be exceedingly difficult. One of the best figured series in which to trace the homology of poles is that shown by Repiachoff ('80, Taf III.) for Bowerbankia. So far as the figures go, one would conclude that Figure 10 A and its predecessors were oriented in the opposite direction to Figure 11 and its successors, which would result in placing the pole of ingression (Fig. 9) at the aboral pole of the larva, — the pole which here, as in all other Gymnolæmata, and, I believe, in Phylactolæmata also, gives rise to the primary polypide. I have given above additional evidence for this conclusion, in my argument to prove the homology of the larvæ and larval organs in Phylactolæmata and Gymnolæmata.

The polypides arise in Phylactolœmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolœmata. The pole of ingression, or the region of the lips of the blastopore, must be regarded as being a region of less pronounced differentiation than the rest of the gastrula. Its cells cannot be said to be either ectodermal or entodermal. It is an interesting fact, that it is just these indifferent cells — not yet either ectoderm or entoderm — that give rise to the inner layer of the polypide, from which organs usually considered ectodermal as well as those considered entodermal arise.

My conclusion, then, the objections to which I fully realize, may be stated in the following words: *The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore. Such cells are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.*

Just when and where, on this hypothesis, the differentiation into ectoderm and entoderm occurs, is an important question; but unfortunately I cannot answer it decisively. It may be pointed out, however, that it has now been shown for most Ectoprocta that the lining of the middle part of the alimentary tract is formed independently of the œsophagus, and by an actual or potential outpocketing of the primitive simple sac of the bud. In Endoprocta there is a similar outpocketing, which, however, arises in connection with the œsophagus, and is formed independently of the rectum.

This is perhaps the proper place to call attention to the fact that the mesodermal outer layer of the bud has a very embryonic character at the budding region. This is indicated by the fact, that in Phylactolæmata (in which group alone I have studied the subject) eggs always arise from that part of the cœlomic epithelium which lies in the budding region (cf. Plate XI. Fig. 93). In Pyrosoma, also, according to the researches of Seeliger ('89, pp. 598–602) the mesoderm of the budding region, the stolon, gives rise to eggs. The same condition seems to exist in other Tunicates.

III. On some Characteristics of Gemmiparous Tissue.

In the preceding part of this paper the words "embryonic tissue," "undifferentiated tissue," have often recurred, and they are terms in wide usage in modern zoölogy. I do not know of any attempt to define further the real character of this tissue, nor to give its more detailed characteristics, other than that usually employed in the term *plasmareich*, or "rich in plasma." The persistence of yolk granules is, as Nussbaum ('80, pp. 2–14) and Goette ('75, pp. 31, 32, 831) have shown in the case of amphibian embryos, indicative of the *embryonic* condition of cells, when these have been derived from an egg filled with yolk.

It is very far from my purpose to go into a detailed discussion of the significance of embryonic tissue, for which I am not yet fitted; nevertheless, I wish to call attention to the minuter characters of gemmiparous tissue as I have found it in Phylactolæmata and Paludicella. I have described it in some detail in preceding pages.

First, then, gemmiparous tissue seems to stain more deeply than non-gemmiparous tissue in the same section. This character has been repeatedly observed before by others, and Braem calls attention to it several times. I have already described how I found, by the use of high powers, that much of this depth of stain was due to the unusually large number of deeply staining granules scattered through the cell, but chiefly gathered about the nucleus (Figs. 6, 17, 18, etc.). So marked is the greater depth of the stain around the nuclei, that, with a power so low that the nuclei are hardly distinguishable, their position is indicated by a deeply staining band.

Secondly, gemmiparous tissue, as I have found it in the cases referred to, is distinguished by the possession of large cells, nuclei, and nucleoli. I had already noticed this fact in my studies on budding in Cristatella, and I find that Braem has figured the nuclei in the budding region as larger than the average (cf. Braem, '90, Taf. VII. Figs. 86, 88–90). My own figures show this repeatedly (Plate I. Figs. 3, 4, 5, 6, Plate II. Figs. 15, 17, Plate XI. Fig. 99, etc.). I have also noticed this to a certain extent in the marine Bryozoa, but, since the cells of the latter are smaller, and as I did not succeed in obtaining from them sections so satisfactorily stained, the results are not so reliable. In attempting to obtain an explanation of this phenomenon one involuntarily recalls to mind the condition in young egg cells, where the nucleus attains a relatively enormous size. This great size of the nucleus in young egg cells is explained by Korschelt ('89, p. 92) as due to its participation in the trophic activity of the cell: "Sein grösster Umfang fällt in die Zeit des energischen Wachsthums der Eizelle." So in the gemmiparous regions the large size of the nuclei must be considered as connected with the growth of the cells.

But if the growth of the cells is accompanied by a rapid ingestion of food material (which the larger nucleus implies), some evidence of that fact should be observed in the cells themselves in the presence of food granules. Such food material in rapidly growing ovarian egg cells lies near the nucleus. Stuhlmann ('87, pp. 13, 14) describes such a condition in the ovary of Zoarces. "Neben dem Keimbläschen, jedoch ein klein wenig von seiner Membran entfernt, bilden sich an verschiedenen Stellen jetzt eigentümliche Verdichtungen des Protoplasmas, die sich ein wenig stärker mit Saffranin färben als das Zellplasma." Such a thickening of the protoplasma is represented in the figures as minute granules. Korschelt ('89, pp. 123–125) mentions several other such instances.

It has seemed to me possible to interpret the stainable granules lying near to the nucleus in gemmiparous tissue as such food material,[1] particularly since we know that food material does exist in the cœlomic epithelium lying next to the cells which are about to divide rapidly and to give rise to the inner layer of the polypide. That food is being taken in by the inner layer cells from the cœlomic epithelium is indicated by the fact that the nuclei of the former cells lie near the latter epithelium (cf. Figs. 15, 17, 18, 28, 56, etc.); for, as Korschelt has shown, the nucleus tends to move towards the centre of activity of the cell. That these granules observed in the cells are food material is indicated by their abundance in cells lying next to the reticulated cells of the cœlomic epithelium (Figs. 6, 28, 56).

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[1] Granules similar to these appear to exist in the protoplasm of all cells. It is their extraordinary abundance in the gemmiparous tissue upon which I lay stress. They have been variously interpreted by different authors. Bütschli ('88, pp. 1469–1472) describes various kinds of stainable granules in Ciliata which are food products, and the general character of which accords with that of the granules referred to above. "Excretion granules" of Ciliata do not stain, according to this author, which is an indication that the bodies in gemmiparous tissue are not such. I am particularly struck by the fact that the food products of Protozoa are chiefly found in parasitic forms, — Gregarinidæ and parasitic Ciliata. These take up food in solution from their hosts exactly as the cells of the body wall of Bryozoa do from the body cavity. Altmann ('90) has recently interpreted similar deeply staining granules in other cells, as "die Elementarorganismen." I can see no reason, on Altmann's theory, for the peculiar distribution of the granules that I have found.

My conclusion, then, is this: *Gemmiparous tissue is a rapidly assimilating tissue, possessing large nuclei because actively assimilating, and staining deeply because full of food material.*[1]

While for Nussbaum, as already quoted (page 71), "indifferent cells" are essential to the reproduction of individuals by non-sexual as well as by sexual methods, Seeliger ('90, p. 596) has concluded that "die Vorgänge bei der Knospung der Bryozoen uns zeigen, wie histologisch sehr bestimmt differenzirte Gewebe einen ganz embryonalen Charakter wiedergewinnen können. Mehr noch als bei der normalen Knospung am freien Stockende ist dieses Vermögen bei der Regeneration der Polypide der Ektoprokten oder der Köpfchen der Pedicellinen ausgebildet. In diesen Fällen sehen wir ein plasmaarmes, äusserest feines Plattenepithel, das über sich eine mächtige Cuticula ausgeschieden hat, sich in kubische und cylindrische plasmareiche Zellen zurückverwandeln und durch eine Einstülpung ein neues Polypid bilden, in welchem schliesslich die mannigfachsten Gewebsformen vertreten sind."

It seems to me that many facts in the budding of Bryozoa are strongly in favor of Nussbaum's hypothesis. On this assumption, we can best understand why in Cristatella there is not an invagination of the ectoderm, and why instead a stolon is formed in the embryo, which passes along at the base of the ectoderm and at intervals gives rise to the inner layer of the body wall. I believe it is because the outer layer of the body becomes so rapidly differentiated by the secretion of the gelatinous balls in its cells as to be incapacitated for the work of building organs. In Plumatella the outer layer of the body wall, which is derived, as Braem has shown, from the neck of the older polypide, retains for a long time its embryonic condition, so that its deeper cells can and do go to form the inner layer of the polypide bud.

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[1] Other observers describe gemmiparous tissue as being either rich in food or deeply staining. Seeliger ('85, p. 588) speaks thus of the mesodermal gemmiparous tissue in Salpa: "Die einzelnen Zellen sind grossblasig, enthalten einen runden Kern und führen Oel- und Fettsubstanzen die als Reservematerial beim Aufbau des embryonalen Leibes weiterhin in Verwendung gelangen." Von Wagner ('90, p. 377) says of the indifferent cells which are being transformed into the new pharynx of dividing Microstoma: "Dieselben nehmen an Grösse zu, . . . indem gleichzeitig ihre Protoplasmaleiber feinkörnig granulirt und für Farbstoffe imbibitionsfähiger werden."

In some sections of gemmules of Esperella fibrexilis, H. V. Wilson, of which Dr. Wilson has very kindly sent me several slides, I find the outer layer of young gemmules, in which the inner layer has been newly formed, stained very deeply. Observed with a Zeiss Apochr. 4.0 mm., Ocs. 8 and 12, the cell contents are seen to be evidently of two kinds, — light and deeply stained. The latter appearance is due, in part at least, to small dark granules, which can be discerned without much difficulty.

On Nussbaum's hypothesis we can best understand why in Paludicella the *Anlagen* of the lateral branches exist from the beginning as cuboidal cells, quite different from those of the rest of the body wall; we can understand why the cell layers of the margins of the stock, the tips of branches, and the ends of stolons from which buds arise, are thicker and more rapidly dividing than the rest of the body wall (cf. Figs. 14, 71, 73, 75); and we can also understand why the regenerating buds always arise from the region of the neck of the degenerated polypide, — the same region from which that degenerate polypide had arisen by budding.

There is no doubt, however, that at times buds do arise from tissue which, as Seeliger says, has lost its cuboidal nature only to regain it. From such tissue apparently the polypide of Figure 79 has arisen; from such tissue certainly, as Seeliger says, do regenerating polypides arise. But is the process by which cuboidal cells become a pavement epithelium one of so fundamental differentiation that, in accordance with Nussbaum's doctrine, we should not expect, under favorable conditions, to see these cells regain their cuboidal form? No doubt we have many other cases in the animal kingdom in which flat epithelial cells regain their cuboidal form. Thus, for instance, among the Bryozoa, Oka ('90, p. 132) has shown how the flat cells of the outer layer of the statoblast begin to thicken again at the return of warmth, and at the beginning of the active assimilative processes, not only at the pole from which the primary polypide is to arise, but also opposite to this.

Many facts indicate that cells may become flattened epithelia, and yet not lose their embryonic character. Maas ('90, pp. 541–544) has recently shown step by step how the columnar ectoderm of the fresh water sponge is forced, on account of the great increase in surface which it is called upon quickly to cover, to become broad and flat. It finally gives rise to an epithelium so flat that its existence was long overlooked, and has been denied by so competent an observer as Goette; and yet in its flattened condition it possesses to a remarkable degree the capacity of sending out pseudopodia-like processes, a condition indicative much less of a high degree of differentiation or specialization, than of an unspecialized, primitive or embryonic condition.

I have already stated (page 65) that the region from which the regenerating buds of Cheilostomes arise, although one of flattened epithelium, is one in which many more nuclei persist than elsewhere in the adult (cf. again Fig. 71). This fact, coupled with the constancy of position of regenerating buds with reference to the degenerated polypide, is to my mind evidence against the assertion that buds arise here from "*histologically very definitely differentiated tissue.*"

As for regeneration in Endoprocta, no one is more competent to speak than Seeliger himself. I am the more surprised, therefore, to find that in Ascopodaria macropus, which is quite closely allied to the species studied by Seeliger ('89), the cells at the part of the stalk immediately below the "head," from which regenerated buds arise, are, as Ehlers's magnificent Pedicellina work shows, very large and cuboidal (Ehlers, '90, Taf. II. Figs. 26–33). I think one may conclude that a similar condition obtains in some cases in Pedicellina, even judging from Seeliger's own drawings, although they are drawn to a scale that is not quite large enough to allow of settling this point (Seeliger, '89, Taf. X. Fig. 35, *a*, Fig. 41, etc.).

If the increase in size of the flattened cells, and their subsequent rapid division and invagination to form a bud, are due to their more active nourishment, it would be difficult to see why certain cells of any region should quickly undergo this modification, while the adjacent cells apparently as favorably situated with reference to the acquirement of food retain their flattened, quiescent condition, if we assumed such favorable situation to be the only requisite. Still less satisfactorily would such an assumption explain the regular position of regenerating buds. It is taking only one step farther back, but, to my mind, a helpful step, to assert that cell proliferation in any region which produces invagination depends upon the capacity of the cells of that region to become better nourished than their fellows. This may evidently be effected by a diminution in the feeding capacity of the surrounding cells, or by an increase in this respect in the growing cells.

IV. Relationships of Endoprocta and Ectoprocta.

I discussed this topic in my earlier paper (Davenport, '90, pp. 132, 133). I have only to add, that later studies have confirmed my opinion of Nitsche's correctness in placing these two groups close together, and in regarding the Endoprocta as nearer the ancestral types. The stages of Figures 25 (Plate III.) and 77 (Plate IX.) probably represent roughly a phylogenetic stage ancestral to both groups of Bryozoa, but most clearly allied to adult Endoprocta. The formation of new tentacles anteriorly and posteriorly in Figure 77, would reproduce the adult Endoproct condition. Two changes lead to the Ectoproct stage: first, the closure of the tentacular corona posteriorly *in front* of the anus (Plate V. Fig. 43), and, secondly, the formation of the pharynx or anterior part of the œsophagus by the growth of the oral tentacles over the floor of the atrium towards the atrial opening. Thus the brain, which lies at the floor of the atrium in Ectoprocta, comes to lie on the pharynx. The pharynx would, upon this assumption, be a new structure, not found in Endoprocta. Such appearances as are exhibited by Figure 77 lead me to retract my former expressed opinion, in which I agreed with Nitsche in saying that the earliest condition of the tentacular corona is a U-shaped one. Rather, the tentacles are formed first on each side of the atrium, and only secondarily grow around the mouth in front, as later they grow in between mouth and anus. The U-shaped stage is therefore not the primary one, but secondary.

The close relationship of Endoprocta and Ectoprocta has recently been doubted by Cori ('90, p. 16), but his chief argument depends upon the dissimilarity of the Endoproct and Ectoproct kidney. Unfortunately, our knowledge of the latter is still very imperfect, and we may well hope for renewed researches in the subject by this skilful investigator.

Ehlers ('90, pp. 149–154) has recently re-expressed his former ('76, p. 132) utterances concerning the lack of homology between the tentacles of Ectoprocta and the "cirri" of Endoprocta. He finds the homologue of the latter in the "Diaphragma" or "Kragen" of Ectoprocta. This is the organ which I have believed to be homologous with Kraepelin's "Randwulst" (which may be Anglicized as marginal thickening), — an organ occurring in all Ectoprocta. It is nothing but the "neck of the polypide," which has sunk below the general level of the body wall. It is always provided with sphincter muscles, and in Ctenostomes forms the base of insertion of the cylindrical or comb-like "collare setosum." It can hardly be that Ehlers refers to this latter structure by the term "Kragen," since this is merely cuticular. In my opinion the "Diaphragma" of Nitsche cannot be homologized with the cirri of Endoprocta, because it is merely a part of the body wall comparable to that part from which the "polypide" of Endoproctous Bryozoa arises, and *beneath* which the tentacles or "cirri" arise. This part of the body wall is provided with a sphincter in Endoprocta as well as Ectoprocta, and by it the atrial cavity may in both cases be closed.

To my mind, the most significant difference between the two groups exists in the fact that the outpocketing to form the stomach arises from the oral end of the future alimentary tract in Endoprocta, and from the anal end in Ectoprocta. One is led to believe that in the ancestral form either two nearly equally important outpocketings from both the oral and anal sides existed, or that the two existing methods are remnants of a method different from either (such as the formation of the whole alimentary tract at once), or, finally, that the Endoproct condition represents the ancestral one, and that the rectal evagination has secondarily become of greater importance in Ectoprocta, and that the oral evagination has become less significant. Oka ('90, pp. 134, 141) has recently asserted that in the polypide buds of the statoblast and adult colony of a Pectinatella of Japan (P. gelatinosa) the œsophagus and stomach are formed by one evagination, which acquires secondary connection with the rectum. This condition reminds one, then, of Endoprocta. I must, however, doubt the accuracy of Oka's conclusions until more satisfactory evidence is forthcoming; the more so, since Pectinatella magnifica, Leidy, presents a method of budding exactly comparable to that in Cristatella and Plumatella, as my own sections show with sufficient clearness.

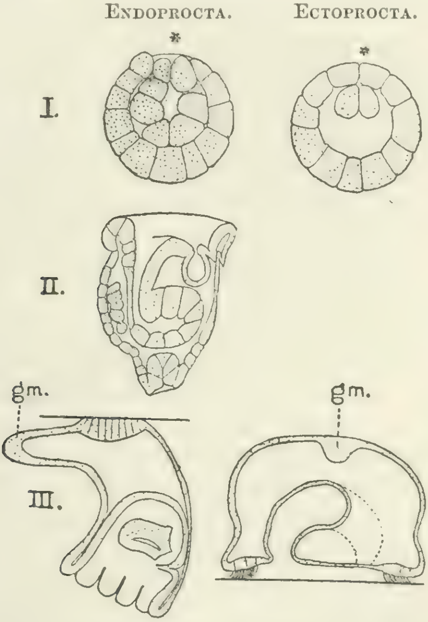
The homology of the Ectoprocta and Endoprocta implies a homology of their larvæ, and demands that the life history of the two groups should be directly comparable.

It is well known from the researches of Hatschek ('77) on Pedicellina, and of Harmer ('85) on Loxosoma, that the surface of the larva which bears the mouth and anus, i. e. its oral side, corresponds with that of the blastopore. How, then, is the oral aspect of the Ectoproct larvæ, which I have tried to show is opposite to the pole of the blastopore, to be homologized with this?

The mouth and anus of the Endoproct larva undergo a rotation after the larva has settled, so that they come to occupy the pole opposite to that at which the blastopore was. This stage of the Endoproct larva is comparable to the whole larval stage of Ectoprocta. I believe the two stages to be homologous, and that, just as polypides are *precociously* formed upon the Phylactolæmatous larva, its larval digestive tract having dropped out from the ontogeny, so the mouth and anus of Gymnolæmata are *precociously* formed on the pole opposite the blastopore, the primitive stage during which they existed at the blastoporic pole having dropped out of the ontogeny.

It is well known from the works of Harmer ('86) and Seeliger ('89), that in Pedicellina, in which the metamorphosis of the larva has been best studied, the stolon arises from the base of the stalk — that is, at the pole where mouth and anus were first formed — at the pole of invagination. I have shown that this is true for Phylactolæmata, and probably for Gymnolæmata.

If the interpretation which I have put on Gymnolæmatous ontogeny becomes confirmed, the larvæ and the budding areas will be homologous throughout all Bryozoa. The following diagrams will explain my idea of the relation of the different ontogenetic stages in the two groups.



The left hand vertical series represents stages in the development of Endoprocta; the right hand one, stages of Ectoprocta. The blastopore (*) is throughout turned upwards in the figures. Stage I. is in both cases a young gastrula. Stage II. is that of the free-swimming larva of Endoprocta. This stage is lost in the ontogeny of Ectoprocta, in which, by abbreviation of larval life, the free-swimming stage corresponds to the condition of the fixed Endoproct after it has undergone its rotation. This stage, or one slightly later, is shown in III. Both larvæ are fixed, the Endoproct by the blastoporic, the Ectoproct by the opposite pole. The position of the stolon, or of the first polypide of the colony produced by non-sexual methods, is represented at *gm.*, near the blastoporic pole.

Summary.

The following general scheme of the budding process in Ectoprocta, derived from my own and other recent studies, may be now drawn up. The references are to pages of this paper.

All Ectoprocta build stocks or corms. The individuals in these are arranged in rows radiating from a centre, — the larva or statoblast, — and are placed one in front of another (Figs. 2, 64^a, 65^a, 67, 71^a, etc.).

New rows or branches are constantly being produced peripherally. There is no dichotomy in the branching (page 86), but the ancestral or median branch gives rise to one or more lateral branches, which in turn become median branches of their part of the stock.

The body wall and polypides of the median branch, as well as the *Anlagen* of lateral branches, arise from a pre-existing mass of embryonic tissue, the gemmiparous mass (pages 72–82). This may exist centrally of the forming region, as in Phylactolæmata, or peripherally, as in Gymnolæmata.

The anal aspect of the polypide is turned towards the gemmiparous mass (page 82).

The outer layer of the body wall in the budding region is one of rapidly assimilating and rapidly dividing tissue ; the inner layer of the body wall becomes filled with food taken from the body cavity in species in which the latter is early cut off by a partition (Paludicella, Bowerbankia, Lepralia ?) ; it shows no tendency to do so in species with a cœnocœl (Phylactolæmata, Alcyonidium).

The first impulse to the formation of the polypide is found in the outer layer of the body wall (excepting when this is highly modified, as in Cristatella), and many cells seem to be involved in its formation from the beginning (pages 8, 56).

This outer layer of the body wall is embryonic tissue, derived from the tip of the stock (margin of the corm) as in Gymnolæmata, or from the neck of pre-existing polypides, as in Phylactolæmata. It is the direct descendant of the gemmiparous tissue of the larva, which in turn has been derived from the region around the blastopore, — in Phylactolæmata certainly, in Gymnolæmata probably (pages 8, 11, 12, 69).

The inner layer of the body wall is also embryonic in the budding region, as indicated by the fact that ova arise near the neck of the polypide, in Phylactolæmata at least (page 68).

The outer mural layer becomes the inner bud layer by invagination, with or without the formation of a cavity. In the former case (many

Gymnolæmata) the mouth of the invagination pocket rapidly closes to give rise to the neck of the polypide (page 56). In the latter case, the cavity of the bud arises only secondarily by a separation of its walls (page 18).

By a rapid growth of the walls of the bud, its distal part, in which the alimentary tract is to arise, is formed. Since this rapid growth occurs earlier at the anal side than at the oral, the rectum is formed first, the stomach last (pages 19, 57).

By an approximation of the lateral walls, alimentary tract and atrio-pharyngeal cavity become separated.

The œsophagus arises as a pocket of the atrio-pharyngeal cavity, and secondarily unites with the stomach (pages 19, 58).

The lophophore arises first as two lateral thickenings of the atrio-pharyngeal wall, then as two lateral folds, whose cavity becomes the ring canal (pages 20, 58),

Tentacles appear on the ridge of the lophophoric fold thus established, and like it are formed first at the sides of the polypide, then anteriorly and posteriorly (pages 22, 59).

The posterior end of the lophophoric ridge is the last to be formed, and, in forming, it cuts off the anal part of the atrium from the intertentacular cavity (pages 23, 62).

The compressed intertentacular cavity becomes circular by change in position of the oral tentacles (pages 24, 62).

The ganglion arises as a depression in the floor of the intertentacular room, and becomes included in the pharynx, which is differentiated by the change in position of the oral tentacles (pages 26, 61).

Muscles and funiculi arise from the cœlomic epithelium of both the body wall and the bud (pages 27–31, 63).

The neck of the polypide may sink to a considerable distance below the general level of the body forming the "Randwulst" of Phylactolæmata or "Diaphragma" of Gymnolæmata (pages 31, 63, 103).

The atrial opening first arises at a late period by separation of the cells of the neck.

The communication plate arises in Paludicella as a circular fold of the layers of the body wall, the mesodermal cells at the centre of which become cuticularized. It is not so completely closed as to prevent communication between the cœlomata of the two individuals it separates.

The mesodermal cells of Paludicella become stored with food material before the formation of the communication plate, and yield it up to the rapidly growing bud.

The regenerated polypides, like the marginal ones, arise in Cheilostomes in a definite position, — on the wall of the operculum from tissue left behind to give rise to the polypide, but not wholly used up in its formation. They arise wholly from the body wall, come to lie next to the "brown body," and cause its disintegration.

The more important theoretical conclusions to which I have arrived are: —

a. There is in every stock or corm of Bryozoa a mass of indifferent cell material, which is derived directly from the indifferent cells of the larva or embryo, and whose function is to form the organs of the different individuals, including the polypides. This mass by constant growth and division affords the embryonic material for lateral branches.

b. The form of the stock and interrelation of individuals is in large part controlled by food supply.

c. The inner layer of the Phylactolæmatous larva represents mesoderm only: the entoderm has become rudimentary through loss of the alimentary function.

d. The polypides arise in Phylactolæmata at the pole of ingression, which is probably homologous with the aboral pole of Gymnolæmata.

e. The inner layer of the polypide bud is composed of cells derived from the rim of the blastopore, and they are to be regarded as still indifferent, and as first becoming differentiated into ectoderm and entoderm in the formation of the young polypide.

f. Gemmiparous tissue is a rapidly assimilating tissue possessing large nuclei because actively assimilating, and staining deeply because full of food material.

g. The Endoproct and Ectoproct larvæ are to be compared by assuming that the act of rotation of the axes occurring in the former has been leaped over in the ontogeny, the mouth and anus arising at once on the pole opposite the blastopore.

Cambridge, Mass., June 1, 1891.

LITERATURE CITED.

Agassiz, A.

'63. On Alternate Generation in Annelids, and the Embryology of Autolytus cornutus. Bost. Jour. Nat. Hist., VII., p. 384.

Allman, G. J.

'56. A Monograph of the Fresh-water Polyzoa. viii + 119 pp., 11 pls. London, Ray Society.

'70. The Genetic Succession of Zoöids in the Hydroida. Trans. Roy. Soc. Edinb., XXVI. 1, p. 97.

Altmann, R.

'90. Die Elementarorganismen und ihre Beziehungen zu den Zellen. Leipzig, Veit & Comp. 145 pp., 21 Taf.

Barrois, J.

'77. Recherches sur l'embryologie des Bryozoaires. Travaux l'Inst. Zool. de Lille, I., 305 pp., 16 pls.

'82. Embryogénie des Bryozoaires. Essai, etc. Jour. Anat. et Physiol., XVIII^{e} Ann., p. 124. [Transl. in Ann. and Mag. Nat. Hist., (5), X., p. 265.]

'86. Mémoire sur la métamorphose de quelques Bryozoaires. Ann. Sci. Nat., Zool., (7), I. 1, p. 1.

Braem, F.

'88. Untersuchungen über die Bryozoen des süssen Wassers. Zool. Anzeiger, XI., No. 288, p. 503; No. 289, p. 533.

'90. Untersuchungen über die Bryozoen des süssen Wassers. Bibliotheca Zoologica, Heft 6. 134 pp., 15 Taf.

Bütschli, O.

'83. Protozoa. Bronn's Klassen und Ordnungen des Thier-reichs, Bd. I., Abth. III., Infusoria, etc., pp. 1281–1584.

Chun, C.

'88. Bericht über eine nach den Canarischen Inseln im Winter 1887/88 ausgeführte Reise. Sitzungsber. Akad. d. Wiss. Berlin, XLIV., p. 1141.

Claperède, E.

'70. Beiträge zur Anatomie und Entwicklungsgeschichte der Seebryozoen. Zeitschr. f. wiss. Zool., XXI. 1, p. 137.

Cori, C. J.

'90. Ueber Nierencanälchen bei Bryozoen. Lotos, XI. 18 pp.

Davenport, C. B.

'90. Cristatella: The Origin and Development of the Individual in the Colony. Bull. Mus. Comp. Zoöl. at Harvard College, XX. 4, p. 101.

'91. Preliminary Notice on Budding in Bryozoa. Proc. Amer. Acad. Arts and Sciences, XXV., p. 278.

Dumortier, B. C., et Beneden, P. J. van.

'50. Histoire naturelle des polypes composés d'eau douce, etc. Bruxelles, M. Hayez. 130 pp., 6 pls.

Ehlers, E.

'76. Hypophorella expansa. Ein Beitrag u. s. w. Abhandl. d. königl. Gesellsch. d. Wiss. zu Göttingen, XXI. 156 pp., 5 Taf.

'90. Zur Kenntniss der Pedicellineen. Abhandl. königl. Gesellsch. d. Wiss. zu Göttingen, XXXVI. 200 pp., 5 Taf.

Eisig, H.

'87. Monographie der Capitelliden des Golfes von Neapel. Fauna u. Flora Golfes v. Neapel, XVI. 906 pp., 37 Taf.

Farre, A.

'37. Observations on the Minute Structure of some of the Higher Forms of Polypi, etc. Philosoph. Trans. Roy. Soc. London, Year 1837, I., p. 387.

Freese, W.

'88. Anatomisch-histologische Untersuchung von Membranipora pilosa L. u. s. w. Archiv. f. Naturgesch., LIV. 1, p. 1.

Goette, A.

'75. Die Entwicklungsgeschichte der Unke. Leipzig, Leopold Vose. 964 pp., 22 Taf.

Grant, R. E.

'27. Observations on the Structure and Nature of Flustræ. Edinburgh New Philos. Jour., (2), III., pp. 107, 337.

Haddon, A. C.

'83. On Budding in Polyzoa. Quart. Jour. Micr. Sci., XXIII., p. 516.

Harmer, S. F.

'85. On the Structure and Development of Loxosoma. Quart. Jour. Micr. Sci., XXV., p. 261.

'86. On the Life-History of Pedicellina. Quart. Jour. Micr. Sci., XXVII., p. 239.

'87. Sur l'embryogénie des Bryozoaires ectoproctes. Arch. Zool. expér. et gen. (2), V., p. 443.

'91. On the British Species of Crisia. Quart. Jour. Micr. Sci., XXXII. 2, p. 127.

Hatschek, B.

'77. Embryonalentwicklung und Knospung der Pedicellina echinata. Zeitschr. f. wiss. Zool., XXIX. 4, p. 502.

Hincks, T.

'80. A History of the British Marine Polyzoa. 2 vols., 8°. (11) + cxli + 601 pp., 83 pls. London, John van Voorst.

Joliet, L.

'77. Contributions à l'histoire naturelle des Bryozoaires des côtes de France. Arch. Zool. expér. et gen., VI. 2, p. 193.

Joyeux-Laffuie, J.

'88. Description du Delagia chætopteri (J. J.-L.). Arch. Zool. expér. et gen., (2), VI., p. 135.

[This is the Hypophorella expansa of Ehlers, '76.]

Jullien, J.

'90. Observations sur la Cristatella mucedo, G. Cuvier. Mém. Soc. Zool. de France, III., p. 361.

Kennel, J. v.

'82. Ueber Ctenodrilus paradilis, Clap. Ein Beitrag u. s. w. Arb. zool.-zoot. Inst. Würzburg, V. 4, p. 373.

Kent, J. S.

'70. On a New Polyzoan, "Victorella pavida," from the Victoria Docks. Quart. Jour. Micr. Sci., X., p. 34.

Kleinenberg, N.

'86. Die Entstehung des Annelids aus der Larva von Lopadorhynchus. Zeitschr. f. wiss. Zool., XLIV. 1, p. 1.

Korotneff, A.

'74. Почкованіе Paludicella. Bull. Roy. Soc. Moscau, X. 2, p. 45. [Russian.]

'75. [Abstract of Korotneff, '74, by HOYER, in Hoffman u. Schwalbe's Jahresber. Anat. u. Phys. f. 1874, III. 2, p. 369.]

'87. Zur Entwicklung der Alcyonella fungosa. Zool. Anz., X., No. 248, p. 193.

'89. Sur la question du développement des Bryozoaires d'eau douce. Mém. Soc. Naturalistes de Kiew, X. 2, p. 393. [Russian.]

Korschelt, E.

'89. Beiträge zur Morphologie und Physiologie des Zellkernes. Zool. Jahrb. (Spengel), Abth. f. Anat. u. Ontog., IV. 1, p. 1.

Kraepelin, K.

'86. Ueber die Phylogenie und Ontogenie des Süsswasserbryozoen. Biol. Centralblatt, VI. 19, p. 599.

'87. Die Deutschen Süsswasser-Bryozoen. Eine Monographie. I. Anatomisch-Systematischer Teil. Abhandl. naturwiss. Verein in Hamburg, X. 168 pp., 7 Taf.

Kükenthal, W.

'85. Ueber die lymphoiden Zellen der Anneliden. Jena. Zeitschr., XVIII., p. 319.

Leidy, J.

'55. Contributions towards a Knowledge of the Marine Invertebrate Fauna of the Coasts of Rhode Island and New Jersey. Jour. Acad. Nat. Sci. Philad., (2), III., p. 135.

Maas, O.

'90. Ueber die Entwicklung des Süsswasserschwammes. Zeitschr. f. wiss. Zool., L. 4, p. 527.

Metschnikoff, E.

'82. Vergleichend-embryologische Studien. Zeitschr. f. wiss. Zool., XXXVII. 2, p. 286.

'83. Untersuchungen über die intracelluläre Verdauung bei wirbellosen Thieren. Arb. aus d. zool. Inst. Wien, V. 2, p. 141.

Nitsche, H.

'69. Beiträge zur Kenntniss der Bryozoen. I. Beobachtungen über die Entwicklungsgeschichte einiger chilostomen Bryozoen. Zeitschr. f. wiss. Zool., XX. 1, p. 1.

'71. Beiträge zur Kenntniss der Bryozoen. III. Ueber die Anatomie und Entwicklungsgeschichte von Flustra membranacea. IV. Ueber die Morphologie der Bryozoen. Zeitschr. f. wiss. Zool., XXI. 4, p. 416.

'75. Beiträge zur Kenntniss der Bryozoen. V. Ueber die Knospung der Bryozoen. Zeitschr. f. wiss. Zool., XXV. Suppl. 3, p. 343.

Nussbaum, M.

'80. Zur Differenzirung des Geschlechts im Thierreich. Arch. f. mikr. Anat., XVIII., p. 1.

'87. Ueber die Theilbarkeit der lebendigen Materie. II. Mitth. Arch. f. mikr. Anat., XXIX. 2, p. 265.

Oka, A.

'90. Observations on Fresh-water Polyzoa (Pectinatella gelatinosa, nov. sp.). Jour. Coll. Sci., Imper. Univ. Japan, IV. 1, p. 89.

Ostroumoff, A.

'86^a. Contributions à l'étude zoologique et morphologique des Bryozoaires du golfe de Sébastopol. Arch. Slaves de Biologie, II., pp. 8, 184, 329.

'86^b. Einiges über die Metamorphose der Süsswasserbryozoen. Zool. Anz., IX., No. 232, p. 547.

'87. Zur Entwicklungsgeschichte der cyclostomen Seebryozoen. Mitth. aus. d. zool. Stat. zu Neapel, VII. 2, p. 177.

Parker, G. H.

'89. Report upon the Organisms, etc. Rept. Mass. State Board of Health on Water Supply and Sewage, I., p. 581.

Pergens, E.

'89. Untersuchungen an Seebryozoen. Zool. Anz., XII., No. 317, p. 504.

Prouho, H.

'90. Recherches sur la larva de la Flustrella hispida (Gray), structure et métamorphose. Arch. Zool. expér. et gen., (2), VIII. 3, p. 409.

'91^b^. Sur le développement de la Membranipora pilosa. Assoc. Française pour l'Avanc. d. Sci., XIX., 2^e^ part., p. 517.

Reichert, K. B.

'70. Vergleichende anatomische Untersuchungen über *Zoobotryon pellucidus* (Ehrenberg). Abhandl. königl. Akad. Wissensch. zu Berlin, a. d. Jahre 1869, II., p. 233.

Reinhard, W. W.

'80. Zur Kenntniss der Süsswasser-Bryozoen. Zool. Anz., III., No. 54, p. 208.

Repiachoff, W.

'75. Zur Entwickelungsgeschichte der Tendra zostericola. Zeitschr. f. wiss. Zool., XXV. 2, p. 129.

'75^a^. Zur Naturgeschichte der chilostomen Seebryozoen. Zeitschr. f. wiss. Zool., XXVI. 2, p. 139.

'78. Ueber die ersten embryonalen Entwickelungsvorgänge bei Tendra zostericola. Zeitschr. f. wiss. Zool., XXX., Suppl., p. 411.

'80. Къ Морфологіи Мшанокъ. 69 pp., 4 Tab., 8°. Odessa, 1880.

Seeliger, O.

'85. Die Knospung der Salpen. Jena. Zeitschr., XIX. 3, p. 573.

'89. Zur Entwickelungsgeschichte der Pyrosomen. Jena. Zeitschr., XXIII., p. 595.

'89^a^. Die ungeschlechtliche Vermehrung der endoprokten Bryozoen. Zeitschr. f. wiss. Zool., XLIX. 1, p. 168.

'90. Bemerkungen zur Knospenentwicklung der Bryozoen. Zeitschr. f. wiss. Zool., L. 4, p. 560.

Semper, C.

'77. Beiträge zur Biologie der Oligochaeten. Arb. zool.-zoot. Inst. Würzburg, IV. 1, p. 65.

Smitt, F. A.

'65. Om Hafs-Bryozoernas utveckling och fettkroppar. Öfversigt Kongl. Vetenskaps-Akad. Förhandl., XXII. 1, p. 5.

'65^a^. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. Öfversigt Kongl. Vetenskaps-Akad. Förhandl., XXII. 2, p. 115.

'67. Kritisk förteckning öfver Skandinaviens Hafs-Bryozoer. Öfversigt Kongl. Vetenskaps-Akad. Förhandl., XXIV. 5, p. 279.

Stuhlmann, F.

'87. Zur Kenntnis des Ovariums der Aalmutter. Abhandl. naturwiss. Verein in Hamburg, X. 48 pp.

Tullberg, T.

'82. Studien über den Bau und das Wachsthum des Hummerpanzers und der Molluskenschalen. Kongl. Svenska Vetenskaps-Akad. Handl., XIX. 3. 57 pp. 12 Taf.

Verrill, A. E.

'73. Report upon the Invertebrate Animals of Vineyard Sound, etc. Rept. U. S. Com. Fish and Fisheries, 1871–72, p. 295.

Vigelius, W. J.

'84. Die Bryozoen, gesammelt während 3. u. 4. Polarfahrt des "Willem Barents." Bijdragen tot de Dierkunde, XI. 104 pp., 8 Taf.

'86. Zur Ontogenie der marinen Bryozoen. Mitth. zool. Stat. zu Neapel, VI. 4, p. 499.

'88. Zur Ontogenie der marinen Bryozoen. Mitth. zool. Stat. zu Neapel, VIII. 2, p. 374.

Wagner, F. v.

'90. Zur Kenntniss der ungeschlechtlichen Fortpflanzung von Microstoma u. s. w. Zool. Jahrb. (Spengel), Abth. f. Anat. u. Ontog., IV., p. 329.

Zacharias, O.

'86. Ueber Fortpflanzung durch spontane Quertheilung bei Süsswasserplanarien. Zeitschr. f. wiss. Zool., XLIII. 2, p. 271.

Zoja, R.

'90. Alcune ricerche morfologiche e fisiologiche sull' Hydra. Bollettino Scientifico, XII. 3, p. 65.

'91. Quelques recherches morphologiques et physiologiques sur l'Hydre. Arch. ital. de Biol., XV. 1, p. 125. [Résumé of Zoja, '90.]

PLATE I.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*gn.*	Ganglion.
cta.	Normal cuticula of adult body wall.	*i.*	Inner layer of bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.
ec'drm.	Ectoderm.	*mu. pyr.*	Pyramidal muscles.
ex.	Outer layer of bud.	*œ.*	Œsophagus (pharynx).
ga.	Stomach.	*rt.*	Rectum.
gm.	Bud.	*ta.*	Tentacle.

All figures are of Paludicella Ehrenbergii.

Fig. 1. Stock of Paludicella Ehrenbergii, viewed as an opaque object. × 4.5.

Fig. 2. Diagram representing the interrelations of individuals in stock shown in Figure 1. *A–H* are individuals of the ancestral (median) branch; *a*, *b*, *c*, etc., lateral branches given off from the ancestral branch to the right; a', b', branches given off to the left; α, β, etc., lateral branches of second order given off in the direction of the distal end of the *ancestral* branch; α', β', etc., given off in the direction of proximal end; a_1', lateral branches of third order — to left.

Fig. 2ª. Diagram of another (smaller) stock. Letters have same significance as in foregoing.

Fig. 3. Cross section of branch near tip, showing the first trace of the bud of the polypide at *ex.*, *i.* × 635.

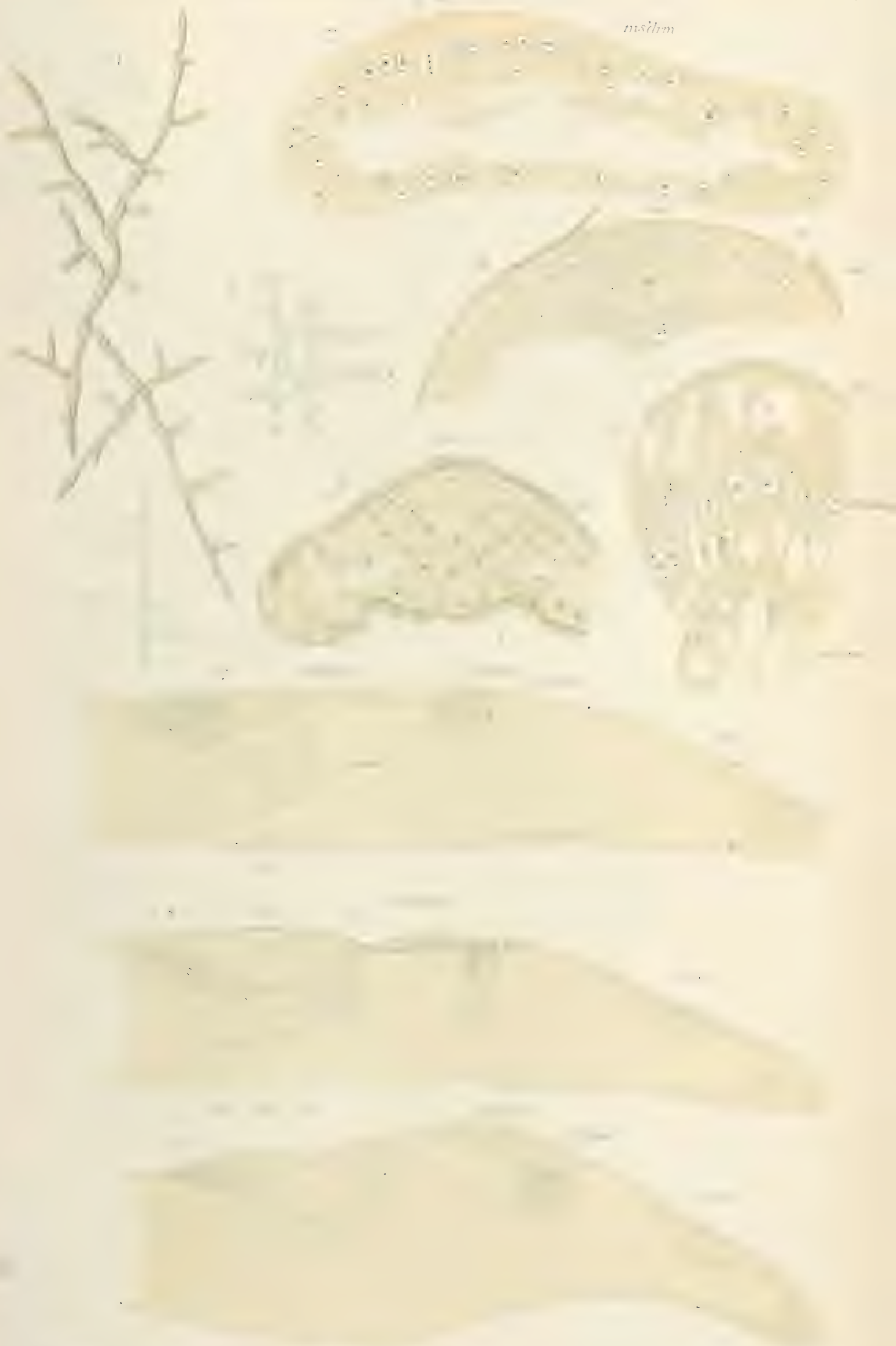
Fig. 4. Cross section of branch near tip, showing bud of polypide slightly older than in Figure 3. × 635.

Fig. 5. Cross section of slightly collapsed branch near tip, showing ingression of cells at *ex.* to form inner layer of bud. × 635.

Fig. 6. Longitudinal section of tip of branch to show cell structure. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1000.

Figs. 7, 8, 9. Optical sections (nearly in sagittal plane) of three tips of branches in successive stages of development, showing relations of young bud, *gm.*, to next older polypide. In Figure 8 the branch is slightly shrunken. × 87.

[illegible] Pl. I.



B. Meisel lith. Boston

PLATE II.

ABBREVIATIONS.

cev. pyd.	Neck of polypide.	*ec'drm.*	Ectoderm.
cta.	Normal cuticula of body wall.	*gm. l.*	*Anlage* of lateral bud.
		kmp'drm.	Kamptoderm.
cta.'	Cuticula secreted by tip.	*ms'drm.*	Mesoderm.

All Figures from preparations of Paludicella Ehrenbergii.

Fig. 10. Surface view of cuticula near the end of a branch at intervals, *a* being nearest the tip, and *d* farthest from it. The branch was stained in Erlich's hæmatoxylin, the color being taken up by superficial cuticula only. × 320.

Figs. 11, 12, 13. Cross sections of the cuticula taken at different distances from the tip, to show the stainable and non-stainable cuticulæ. Figure 11 is from near the tip, Figure 13 farthest from it. × 1000.

Fig. 14. Longitudinal median (sagittal) section through the tip of a branch showing cells of tip and an early stage in the development of the polypide. × 410.

Fig. 15. Cross section of branch showing origin of lateral bud. × 635.

Fig. 16. Longitudinal section of body wall of branch through the point at which a lateral bud is originating. Polypide of ancestral branch is nearly adult. × 635.

Fig. 17. Longitudinal section of body wall from near the tip through the *Anlage* of a lateral bud. × 410.

Fig. 18. Cross section of branch showing histological conditions of *Anlage* of lateral bud. The polypide has reached a stage of development corresponding to that of Figure 36, Plate IV. × 1000.

Fig. 19. Longitudinal section through body wall from the same branch as Figure 17, but farther from the tip. Histological conditions are to be compared with those of Figure 17, which represents a less differentiated condition. × 410.

Fig. 20. Cross section of branch in which the polypide has reached a stage slightly younger than that of Figure 36. To show *Anlage* of two lateral buds with their cuboidal undifferentiated cells. × 410.

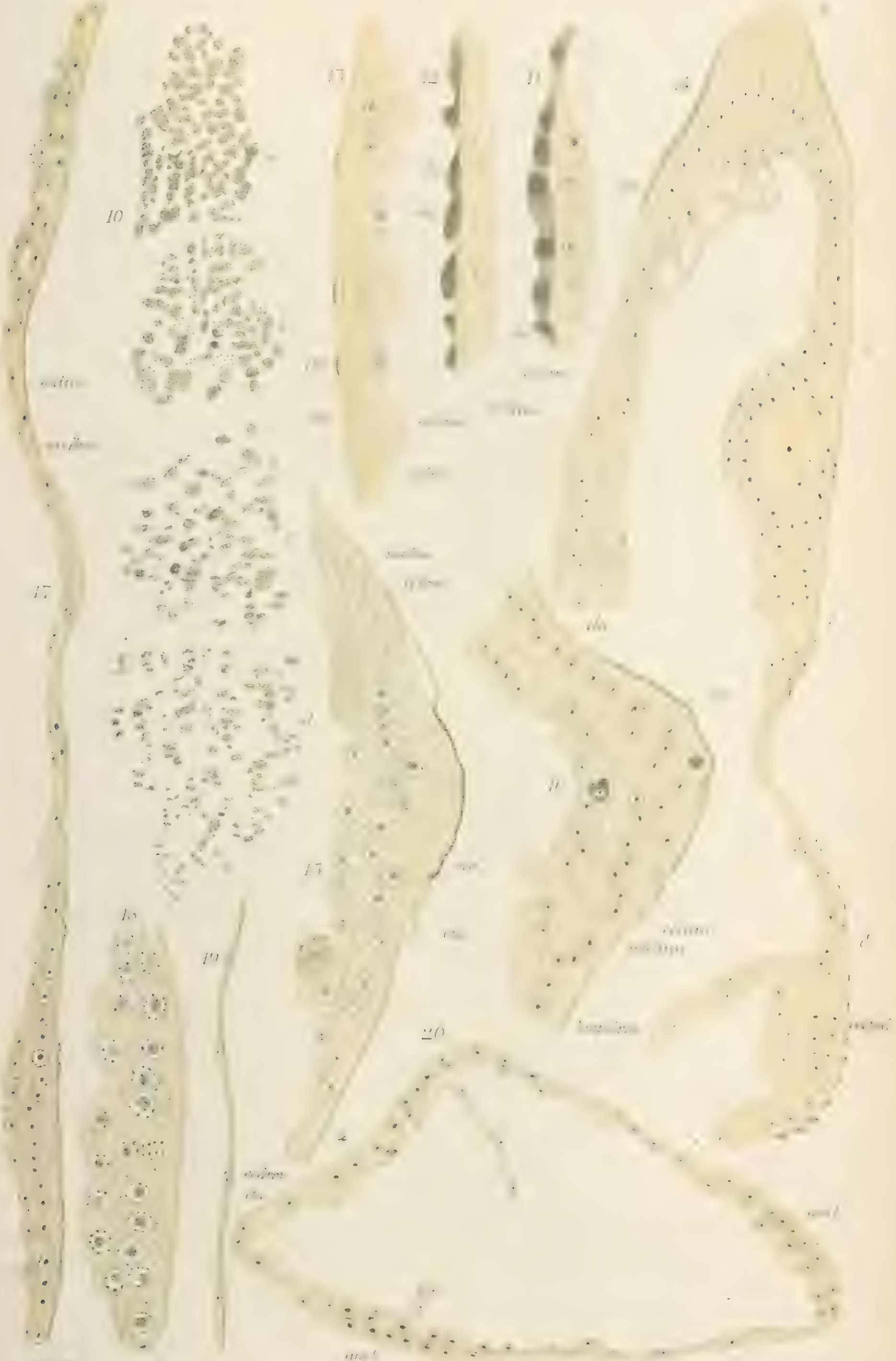

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PLATE III.

ABBREVIATIONS.

An.	Anal side of polypide.	*kmp'drm.*	Kamptoderm.
atr.	Atrium.	*loph.*	Lophophore.
cev. pyd.	Neck of polypide.	*ms'drm.*	Mesoderm.
cl. mu. ret.	Young cells of retractor muscle.	*mu. par.*	Parietal muscle.
cta.	Cuticula.	*œ.*	Œsophagus.
ec'drm.	Ectoderm.	*Or.*	Oral side of polypide.
ga.	Stomach.	*rt.*	Rectum.
gn.	Ganglion.	*vlv. cr.*	Cardiac valve.

All figures from preparations of Paludicella Ehrenbergii.

Figs. 21–25. Longitudinal sections through buds of polypides at successively older stages. The tip of the colony, and therefore the anal aspect of the polypide, is to the right in all cases. All figures × 410.

Fig. 21. Stage of Figure 37 (Plate IV.). Few nuclei in central region.

Fig. 22. Shows rapid growth of bud, chiefly at neck of polypide. The two inner cell layers are about to separate to form the common cavity of atrium and œsophagus.

Fig 23. Beginning of formation of alimentary tract at rectum, *rt.* The row of nuclei separating the atrio-œsophageal cavity from the alimentary tract is due to the fusion of the two inner layers of the bud along this line.

Fig. 24. Rectum and stomach completed. Retractor muscles begin to form.

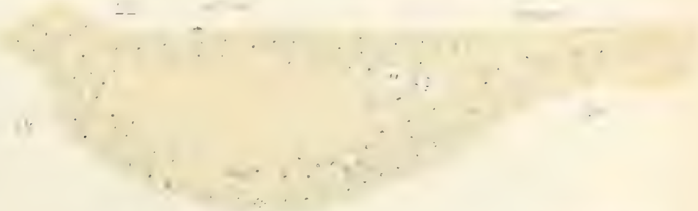
Fig. 25. Lophophore and young tentacles have made their appearance, and œsophagus and pharynx are separated from atrium. Beginning of formation of brain at *gn.*

Fig. 26. Part of cross section of a branch of stage of Figure 30. Parietal muscles, *mu. par.*, occupy a diameter of the section, and are attached to the cuticula. × 635.

Fig. 27. Young parietal muscle at stage of Figure 28. This is one of the pair which in a later stage are found lying together in Figure 26. × 635.

Fig. 28. Cross section of branch showing young polypide, and reticulated vacuolated cells. × 410.

Fig. 29. Bit of body wall, with cuticula separated from underlying ectoderm to show ends of parietal muscles. × 690.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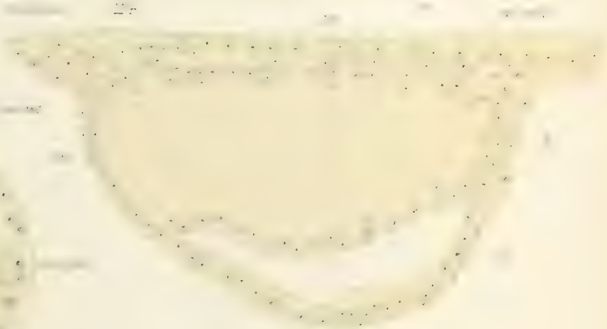
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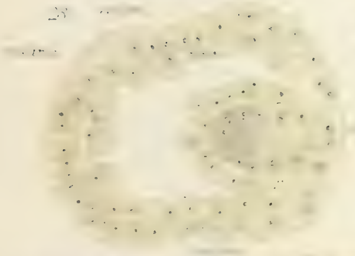

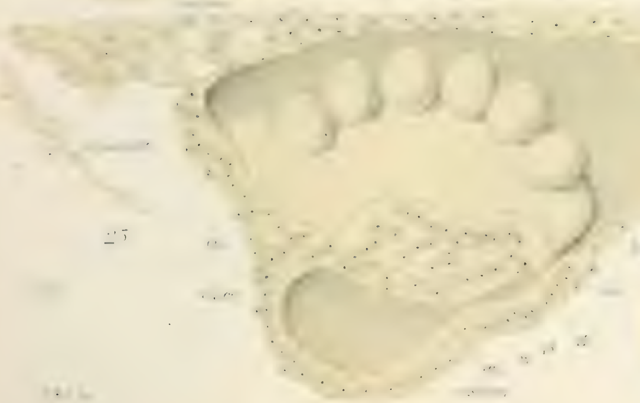
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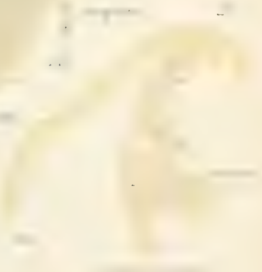


PLATE IV.

ABBREVIATIONS.

An.	Anal side of polypide.	*i.*	Inner layer of bud.
an.	Anus.	*loph.*	Lophophore.
atr.	Atrium.	*ms'drm.*	Mesoderm.
can. crc.	Ring canal.	*mu.*	Muscle fibre in funiculus.
ec'drm.	Ectoderm.	*n.'*	Circumœsophageal nerve.
ex.	Outer layer of bud.	*œ.*	Œsophagus.
fun. inf.	Inferior funiculus.	*Or.*	Oral side of polypide.
fun. sup.	Superior funiculus.	*rt.*	Rectum.
ga.	Stomach.	*vac.*	Vacuole.
gn.	Ganglion.	*vlv. cr.*	Cardiac valve.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 30. Cross section of polypide bud of stage of Figure 24, Plate III. The position is indicated by the line 30, Figure 24. × 410.

Figs. 31–34. Four cross sections of a branch through a young polypide, somewhat younger than that of Figure 25. Figure 31 is nearer the anal, Figure 34 nearer the oral surface. In Figure 34 that part only of the section of the polypide which lies near the body wall is represented. × 410.

Fig. 35. Cross section of branch through polypide of age of Figure 25. To show origin of tentacles and ring canal. × 410.

Fig. 36. Sagittal section of young polypide at period of closure of ganglion, *gn.* × 410.

Fig. 36ª. Bit of same polypide a few sections to one side of plane of Figure 36, showing origin of inferior funiculus. × 410.

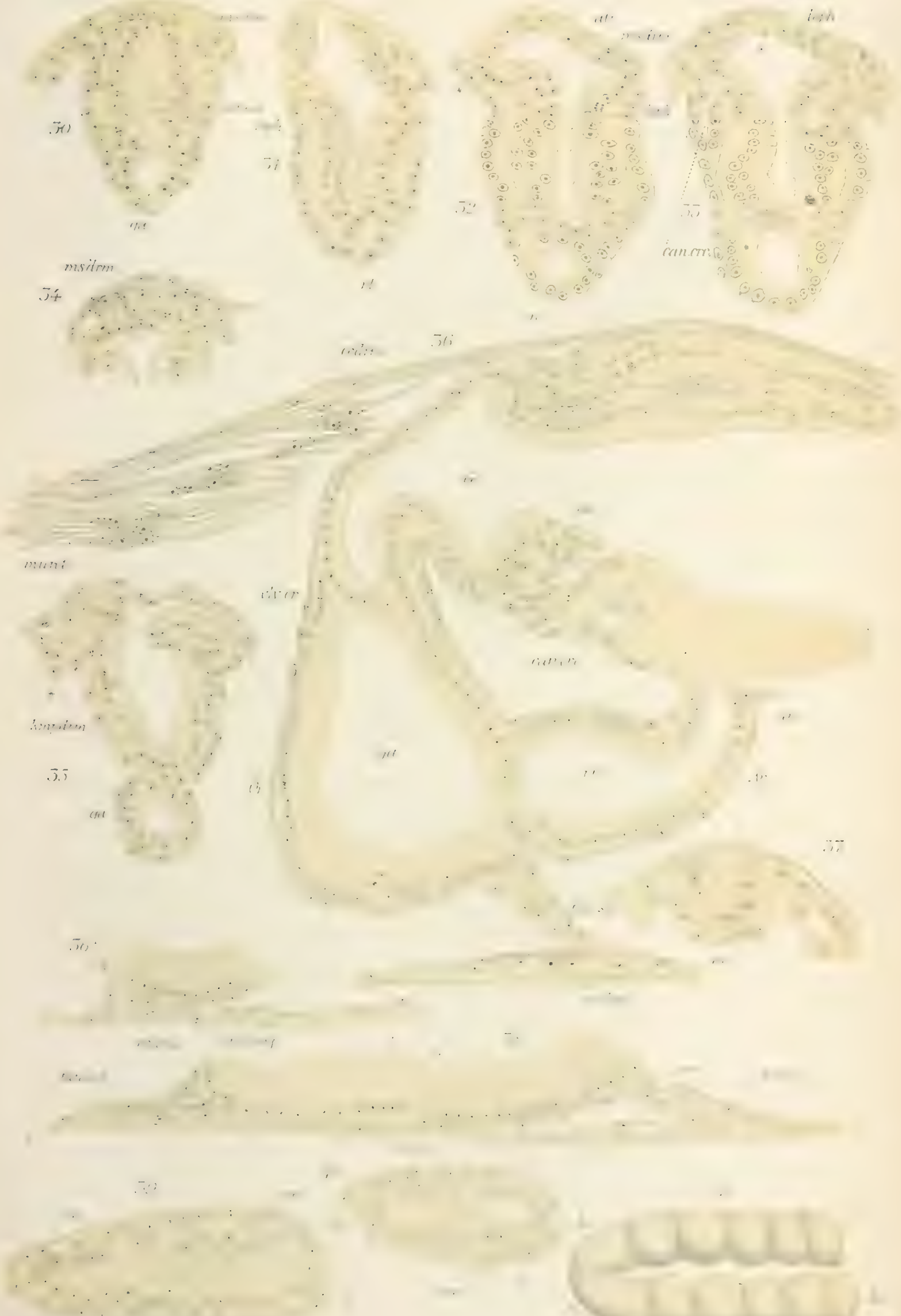
Fig. 37. From cross section of branch showing early stage in development of the bud. × 410.

Fig. 38. From a sagittal section of nearly adult polypide, showing the two funiculi and their muscles. × 410.

Figs. 39 and 40. Two neighboring sections parallel to the body wall through a bud of the stage of Figure 23. Figure 40 lies three sections below Figure 39. Figure 39 shows the atrial cavity, formed as yet only on the anal side. Figure 40 shows the beginning of formation of the alimentary tract at the anal end. Note the vacuolated condition of the mesoderm. × 410.

Fig. 41. Polypide of about the stage of Figure 25 looked at *en face.* The anal tentacles, being turned under, do not appear. To show compressed condition of polypide, and alternating position of tentacles. Cf. Figure 77, Plate IX. × 320.

DAVENPORT. – BUDDING IN BRYOZOA. Pl. IV.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B. Meisel lith. Boston

PLATE V.

ABBREVIATIONS.

an.	Anus.
cev. pyd.	Neck of the polypide.
clr. set.	Collare setosum.
cta.	Normal cuticula of adult body wall.
cta.'	Cuticula secreted by the tip of branch.
ec'drm.	Ectoderm.
kmp'drm.	Kamptoderm.
loph.	Lophophore.
ms'drm.	Mesoderm.
mu. par.	Parietal muscles.
mu. pyr.	Pyramidal muscles.
of. atr.	Atrial opening.
rt.	Rectum.
spht.	Sphincter.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 42. Cross section of branch of age of Figure 37, Plate IV., to show origin of primary parietal muscles. × 410.

Figs. 43 and 44. Successive sections through a polypide slightly older than that of Figure 25, cut perpendicularly to the long axis of the branch. During this period the lophophore becomes more nearly circular, and its aboral ends meet oralwards of the rectum, *rt.* Figure 44 is nearer the tip of the branch. × 410.

Fig. 45. Axial section of neck and atrial opening of polypide just sufficiently developed to be capable of extrusion. Shows the collare setosum in place. × 410.

Fig. 46. Section of communication plate cut across the branch. Two sections (10 μ) above Figure 51. × 635.

Figs. 47–49. Three stages in the development of the communication plates. Longitudinal sections of the branch. In Figure 47, the polypide has reached the stage of Figure 22; in Figure 48, the stage of Figure 23; and in Figure 49, the stage of Figure 24. × 635.

Fig. 50. Longitudinal section through neck of young polypide, showing the sinking of the neck below the general surface of the body, and the method of forming the inner cuticula of neck. × 390.

Fig. 51. Cross section of branch through communication plate. The left side of the section includes the cuticula and the underlying flat ectodermal layer. The right side cuts a little lower into the mesodermal cells. × 635.

DAVENPORT – BUDDING IN BRYOZOA.

PLATE VI.

ABBREVIATIONS.

an.	Anus.
can. crc.	Ring canal.
cev. pyd.	Neck of the polypide.
cl. rtl.	Reticulated cells.
cta.	Normal cuticula of adult body wall.
cta.'	Cuticula secreted by tip.
ec'drm.	Ectoderm.
ex.	Outer layer of bud.
gm.	Bud.
gn.	ganglion.
i.	Inner layer of bud.
kmp'drm.	Kamptoderm.
la. comn.	Communication plate.
ms'drm.	Mesoderm.
mu. par.	Parietal muscles.
mu. pyr.	Pyramidal muscles.
n.'	Circumœsophageal nerve.
œ.	Œsophagus.
rt.	Rectum.
vac.	Vacuole.

All figures from preparations of Paludicella Ehrenbergii.

Fig. 52. Cross section of a branch through a polypide slightly older than that shown in Figure 36. The section passes through the brain and whole extent of the ring canal, together with its opening into the cœlom. × 635.

Fig. 53. Next section below Figure 52 of same series; showing the beginning of the circumœsophageal nerve ring. × 635.

Fig. 54. Shows connection of mesodermal cells of body wall, *ms'drm*, with those of the outer layer of bud, *ex*. × 1030.

Fig. 55. Origin of the secondary parietal muscle cells from mesoderm of body wall. × 635.

Fig. 56. Histological conditions of the budding regions. The cells have large nuclei, the mesodermal cells are vacuolated and rapidly dividing; the cells of the bud are densely granular. Zeiss, $\frac{1}{18}$ oil immersion, Oc. 1. × 1070.

Fig. 57. Normal vacuolated cell, full of food particles. × 1030.

Fig. 58. Longitudinal section of young lateral branch, showing highly reticulated character of mesoderm, and nearly complete formation of communication plate. × 410.

Fig. 59. Reticulated cell, showing one of the pseudopodia-like processes which frequently appear on them, projecting into the cœlom. × 1030.

Figs. 60–62. Three successive sections from a series across the tentacles of a polypide which has 15 tentacles, and is of about the stage of Figure 36. The odd tentacle (*) is shorter than the others, and lies opposite the rectum, *rt*. × 295.

Fig. 63. Cross section of branch through neck of polypide of about the age of Figure 36. Shows also the young pyramidal muscles. × 410.

DAVENPORT. – BUDDING IN BRYOZOA.

PLATE VII.

For explanation of notation employed on this plate, see page 41.

Fig. 64. Outline drawing of one of the lateral "fans" of *Bugula turrita*, taken from the axis of the colony and spread out flat on the slide. × ca. 12.

Fig. 64ª. Diagram showing arrangement of individuals in Figure 64.

Fig. 65. Outline drawing of one of the lateral branches of a stock of *Crisia eburnea*, spread out flat on the slide. × 16.

Fig. 65ª. Diagram showing arrangement of individuals in Figure 65.

Fig. 66. Part of stock of *Bugula flabellata*. × 10.

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PLATE VIII.

ABBREVIATIONS.

op.	Operculum.	*pyd. rgn.*	Regenerated polypide.
pyd. dgn.	Degenerated polypide.		

Fig. 67. Diagram to show interrelation of individuals in the corm, Figure 69.

Fig. 68. A part of a corm of *Membranipora pilosa*, to show regular arrangement, with a single median branch, each of whose individuals gives rise to two lateral branches. The * indicates margin of frond on which stock was growing. × ca. 8.

Fig. 69. Young corm of *Flustrella hispida*, to show arrangement of individuals. × 10.

Fig. 70. Young corm of *Membranipora pilosa*, with several median branches, showing regular arrangement. The marginal ones alone give rise to lateral branches. × 10.

Fig. 71. Young corm of *Lepralia Pallasiana*, showing arrangement of individuals. On the left, the nuclei of the cells of the body wall are shown, to indicate the inequality of their distribution. On the right, nuclei are omitted. At *pyd. rgn.* a regenerating polypide is seen, on the operculum. × 43.

Fig. 71^{a}. Plan of Figure 71.

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PLATE IX.

ABBREVIATIONS.

An.	Anal side of polypide.	*lu. gm.*	Lumen of bud.
atr.	Atrium.	*marg.*	Margin of corm.
can. crc.	Ring canal.	*ms'drm.*	Mesoderm.
cev. pyd.	Neck of the polypide.	*n.'*	Circumœsophageal nerve.
cta.	Cuticula.	*œ.*	Œsophagus.
ec'drm.	Ectoderm.	*Or.*	Oral side of polypide.
ex.	Outer layer of bud.	*rt.*	Rectum.
ga.	Stomach.	*sep.*	Wall of zoœcium in the corm.
gm.	Bud.	*sol.*	Sole of the corm.
gn.	Ganglion.	*tct.*	Roof of the corm.
i.	Inner layer of bud.		

Fig. 72. Longitudinal vertical section through the peripheral part of the corm of *Lepralia Pallasiana*, showing the margin of the corm and two zoœcia, the older of which contains a polypide. × 160.

Fig. 73. Longitudinal vertical section through the margin of a corm of *Lepralia Pallasiana*, showing the two layers of this region and the origin of the polypide. × 410.

Fig. 74. Young regenerating polypide of *Flustrella hispida*. The section passes through the sagittal plane. × 380.

Fig. 75. Vertical section through margin of corm of *Flustrella hispida*, to show origin of polypide. × 410.

Fig. 76. Sagittal section through young polypide of *Flustrella hispida*, to show early stage of development of alimentary tract. × 410.

Fig. 77. Superficial view of young polypide from upper surface of corm of *Flustrella hispida*, showing young tentacles and their relation to the anus (at *atr.*). × 320.

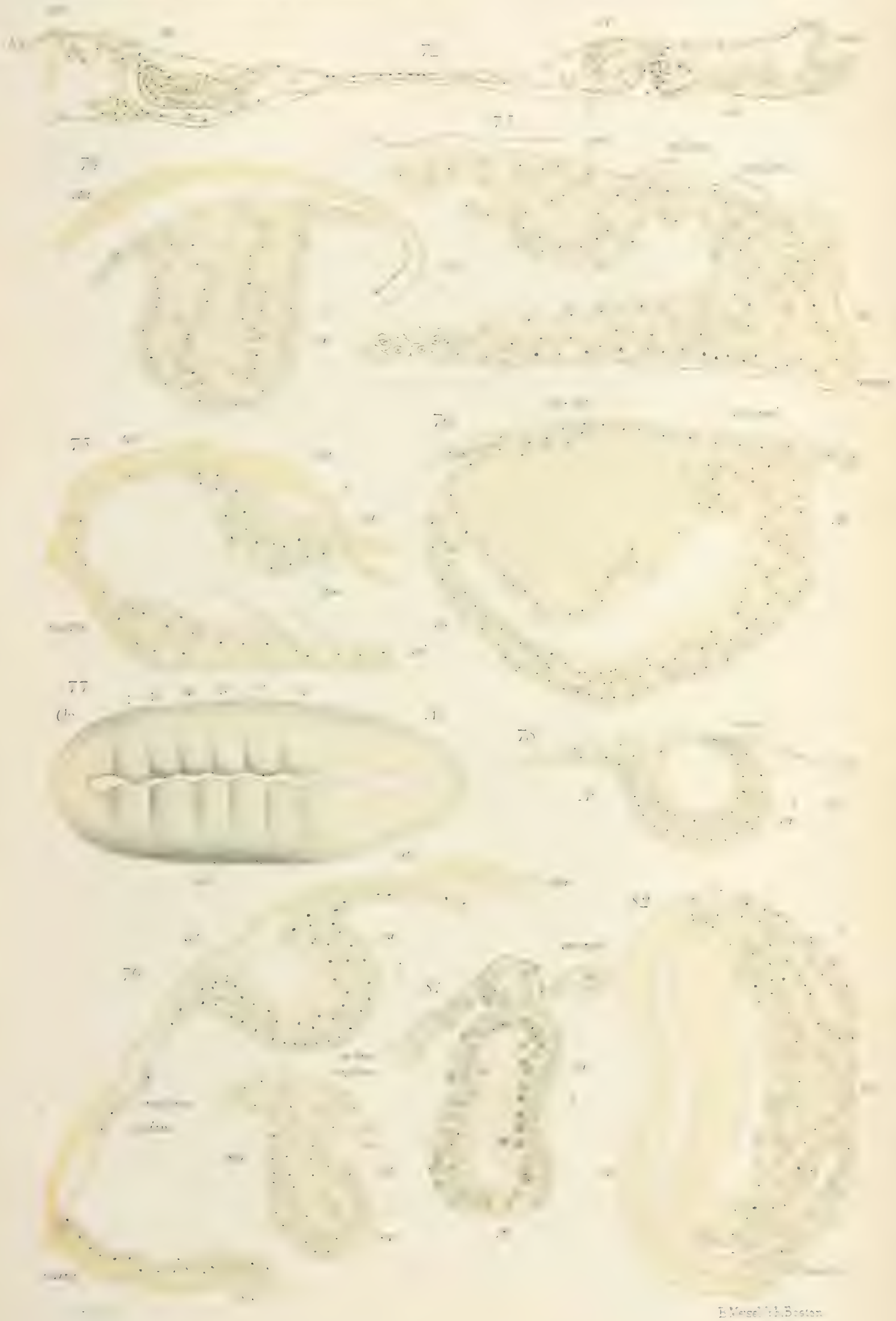
Fig. 78. Bud of polypide of *Flustrella hispida* at the time of closure of the pore of invagination. × 390.

Fig. 79. Radial section through margin of corm of *Flustrella hispida*, showing bud of polypide. × 410.

Fig. 80. Young polypide of *Flustrella hispida*. × 380.

Fig. 81. Bud of *Lepralia Pallasiana* immediately before the formation of alimentary tract, showing relation of the rectal pocket (*rt.*) to the atriopharyngeal cavity above. × 410.

Fig. 82. Section through polypide, through lately formed brain and circumœsophageal nerves (*n.'*) growing around œsophagus (*œ.*). × 410.



B. Meisel lith. Boston

PLATE X.

ABBREVIATIONS.

An.	Anal side of polypide.	*kmp'drm.*	Kamptoderm.
an.	Anus.	*lu. gn.*	Lumen of the ganglion.
atr.	Atrium.	*ms'drm.*	Mesoderm.
can. crc.	Ring canal.	*mu.*	Musculature of œsophagus.
cev. pyd.	Neck of polypide.	*mu. ret.*	Retractor muscle of polypide.
cœ.	Cœcum.	*œ.*	Œsophagus.
cta.	Cuticula.	*op.*	Operculum.
di'sep.	Wall of zoœcium in the corm.	*Or.*	Oral side of polypide.
ec'drm.	Ectoderm.	*or.*	Mouth.
ex.	Outer layer of bud.	*pyd. dgn.*	Degenerated polypide, "brown body."
fun.	Funiculus.	*rt.*	Rectum.
ga.	Stomach.	*ta.*	Tentacle.
gn.	Ganglion.		
i.	Inner layer of bud.		

Fig. 83. Sagittal section through young polypide of *Escharella variabilis.* × 320.

Fig. 84. Regenerated polypide of *Lepralia Pallasiana* on operculum (*op.*). × 380.

Fig. 85. Cross section of pharynx of adult polypide of *Escharella variabilis,* showing perforated cell walls. × 635.

Fig. 86. Sagittal section of young polypide of *Lepralia Pallasiana,* showing formation of brain. × 320.

Fig. 87. Section parallel to sole of a corm of *Escharella variabilis* at about the stage of Figure 86, showing atrium, ganglion, and rectum. × 430.

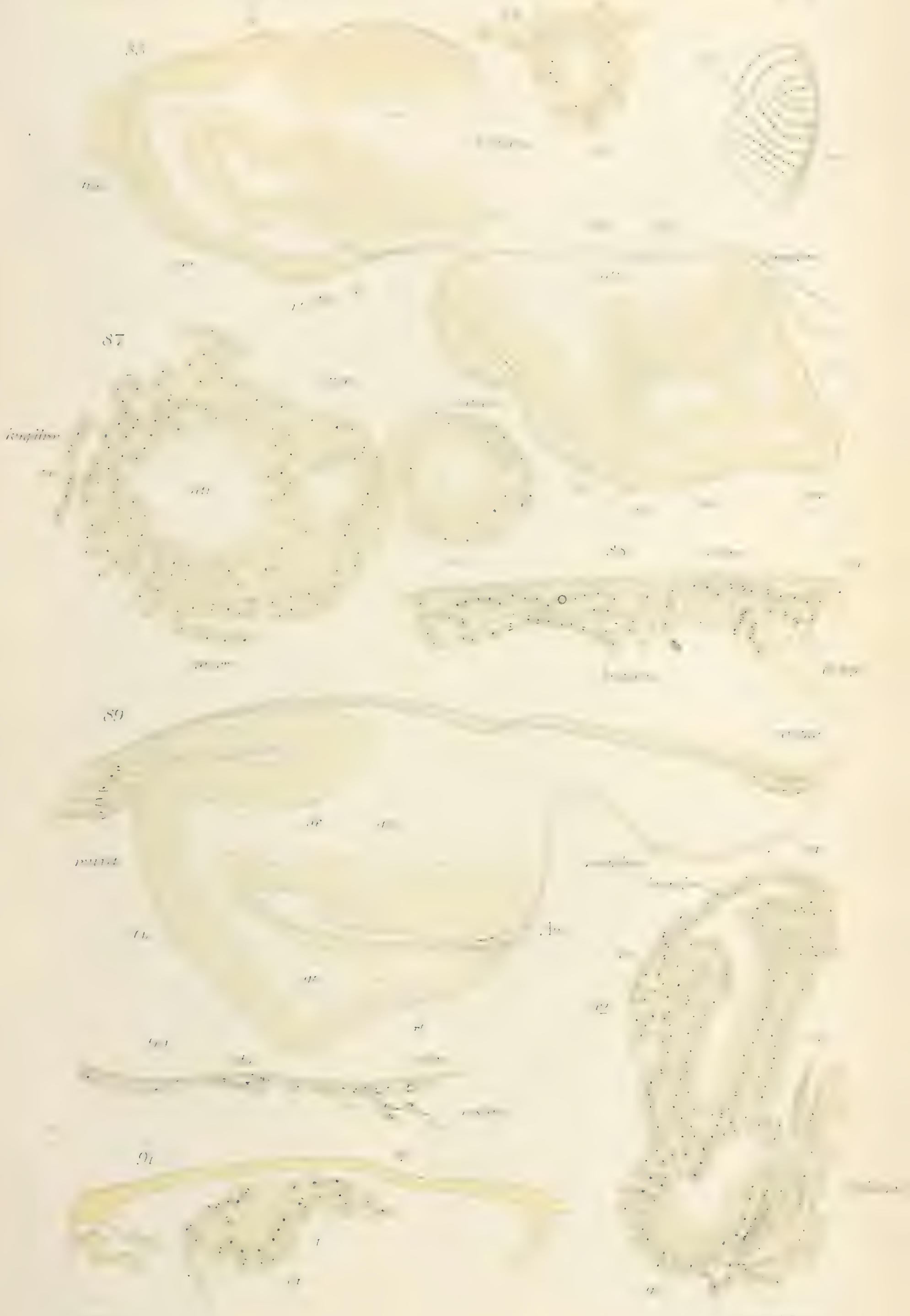
Fig. 88. Vertical section through a bit of roof of corm of *Escharella variabilis* at neck of polypide, showing also the region of future operculum and of origin of future regenerated buds. Compare with Figure 90. × 410.

Fig. 89. Sagittal section of young regenerated polypide of *Flustrella hispida* intermediate in age between Figures 86 and 83. Shows the origin of the ganglion and rotation of the oral tentacles. × 320.

Fig. 90. Vertical section of a bit of body wall from same individual as Figure 88, to show the comparatively less embryonic condition of cells here than at neck of polypide. × 410.

Fig. 91. Operculum of *Lepralia Pallasiana* cut perpendicularly to surface, showing origin of a regenerating polypide. Body wall somewhat shrunken from cuticula. × 410.

Fig. 92. Section through a regenerated polypide of *Escharella variabilis,* showing relations of alimentary tract to "brown body" (*pyd. dgn.*). × 410.



B. Meisel, lith. Boston.

PLATE XI.

ABBREVIATIONS.

cev. oœ.	Neck of oœcium.	*ms'drm.*	Mesoderm.
cœl.	Cœlom.	*oœ.*	Oœcium.
ec'drm.	Ectoderm.	*ov.'*	Oöblasts.
en'drm.	Entoderm.	*pyd.*	Polypide.
ex.	Outer layer of bud.	*sto.*	Stolon.
i.	Inner layer of bud.	*tct.*	Roof of stock.
lu. gm.	Lumen of the bud.		

Fig. 93. A portion of a longitudinal section through a young stock of *Plumatella polymorpha*, about two weeks after hatching from statoblast (killed 12th May, 1890), showing the body wall just analward of the neck of a young polypide (*pyd.*), at the oral side of which a younger bud has already arisen. The inner (mesodermal) layer of the body wall shows oöblasts (*ov.'*) in various stages of development. × 600.

Fig. 94. Longitudinal section of oœcium of *Cristatella* showing embryo which is giving rise to the cœlomic epithelium by ingression of cells at its proximal pole, — i. e. the pole nearest the neck of the oœcium. There are in the next section two other cells in the cavity of the blastula, one of which appears degenerate in that it contains a huge vacuole, and has no distinct nucleus, the chromatic substance lying scattered loose near the cell wall. × 600.

Fig. 95. Longitudinal section through oœcium of *Cristatella* and its contained embryo. One polypide bud and the stolon (*sto.*) are shown here. There are two other buds in the embryo further developed than this one, lying to one side of it, and on the side of each of these buds is the *Anlage* of another. The *stolon* is seen to be well developed, lying between the ectoderm and mesoderm throughout the region bounded by the three older buds, and extending as a zone beyond them, and even beyond the *Anlage* of the youngest polypides. The embryonic tissue thus forms a disk about 75 × 150 μ in extent. × 390.

Fig. 96. Transverse section of oœcium of *Plumatella*, showing origin of first polypide. Compare with Figure 99, which represents an earlier stage. × 390.

Fig. 97. Longitudinal section through oœcium and contained embryo of *Cristatella*. The stolon is already cut off from the ectoderm. This stage immediately follows that of Figure 101, Plate XII. The forming bud is that of the first polypide. × 390.

Fig. 98. Oblique section through oœcium of *Plumatella*, showing a later stage in development of the inner layer of the larva (cf. Fig. 94). × 600.

Fig. 99. Longitudinal section of oœcium and contained larva of *Plumatella*. The bud shown at *i.*, *ex.* is the first in the colony. An incipient (second) bud is shown five sections to one side in the region indicated by an asterisk. × 410.

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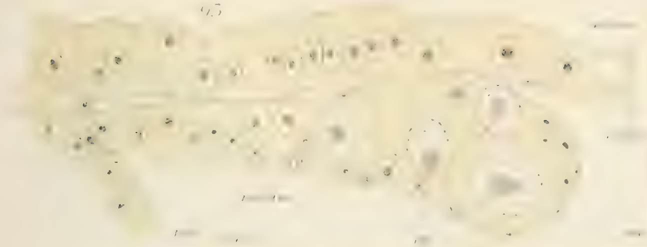

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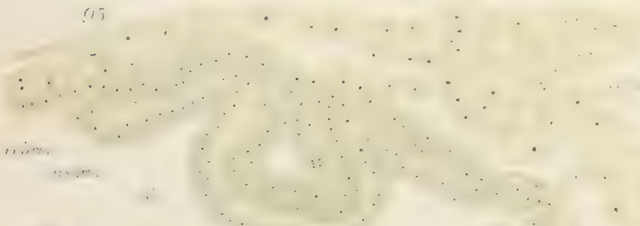

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B. Meisel lith. Boston

PLATE XII.

ABBREVIATIONS.

ec'drm.	Ectoderm.	*ms'drm.*	Mesoderm.
ex.	Outer layer of bud.	*oœ.*	Oœcium.
i.	Inner layer of bud.	*sto.*	Stolon.
lu. gm.	Lumen of the bud.		

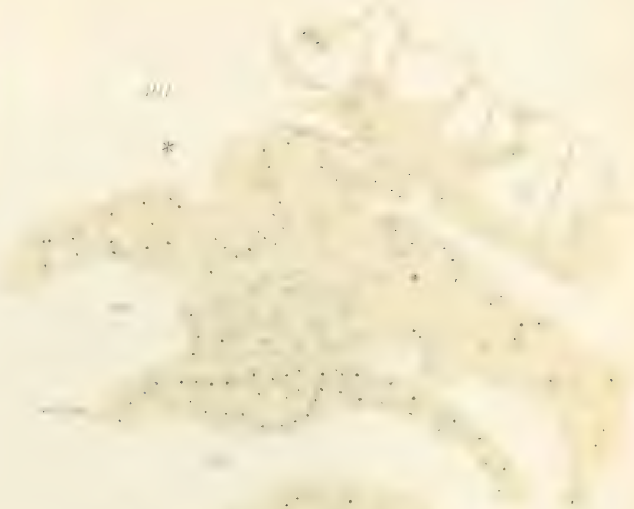
Fig. 100. Longitudinal section of a larva of *Plumatella polymorpha,* in which the two layers are established; the pole of ingression is directed upward, on the plate.

Fig. 101. Section of upper part of zoœcium of *Cristatella mucedo,* with its contained larva. Showing the formation of the stolon at the pole of ingression and the attachment of this pole to the placenta-like neck of the oœcium (*). × 390.

Fig. 102. Section through an oœcium of *Cristatella,* with its contained larva. One polypide is already established, and a second is arising. The two are the only buds in the larva. On the left of the older bud the stolon is seen to be intruding itself between the ectoderm and mesoderm of the larva. × 390.

Fig. 103. Section through the two oldest polypides of the *Cristatella* larva, together with the stolon. This larva contains one other less developed bud at one side of these two. × 390.

Fig. 104. *Plumatella polymorpha.* Stage of first bud later than that shown in Figure 96, exhibiting pore of invagination closed by overgrowth of ectoderm. × 390.



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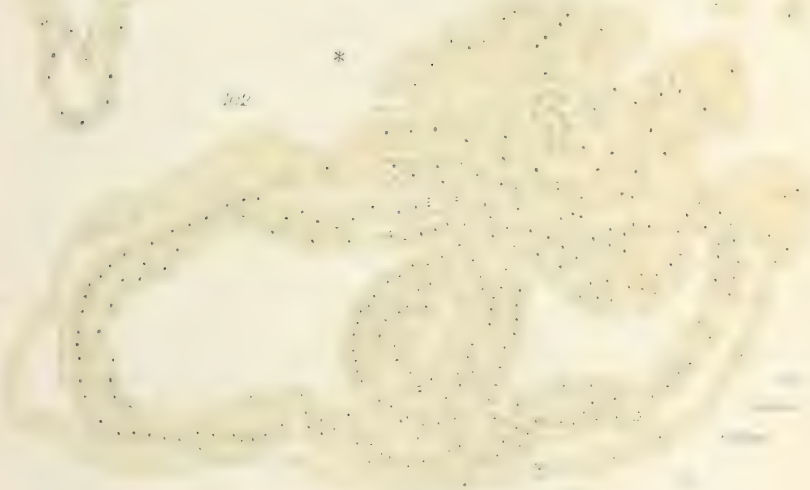

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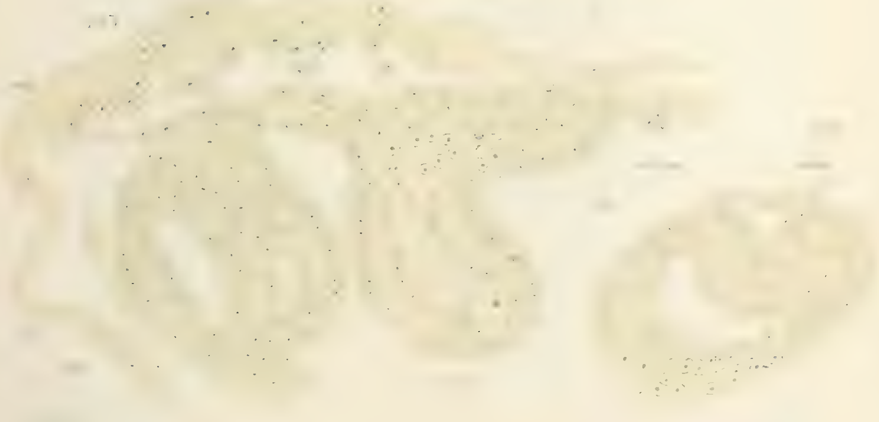

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B. Meisel lith. Boston

No. 2. — *The Gastrulation of Aurelia flavidula, Pér. & Les.*

By Frank Smith.[1]

Preceding the appearance of Goette's ('87) publication in 1887 upon the development of Aurelia aurita and Cotylorhiza tuberculata, the gastrulation of Aurelia had been regarded, in the light of the studies of Kowalewsky, Haeckel, Claus, and others, as the result of invagination or at least of a process nearer to invagination than to any other method of gastrulation.

Goette's work seemed to show, however, that, instead of an invagination, there is an ingression of cells to form the entoderm, and that the first result of this ingression is the production of a solid gastrula, or sterrogastrula, which is only subsequently hollowed out, and is put into communication with the exterior through the formation of a prostoma at a still later period. Recently, in a paper dealing especially with the development of Cotylorhiza tuberculata, Claus ('90) reaffirms the position taken in his previous paper ('83), in which the gastrulation in Aurelia was represented as being simply a modification of invagination. In recent papers by Hamann ('90) and McMurrich ('91), Goette's views are adopted, and form part of the basis for statements that, in the development of the Scyphomedusæ, invagination, instead of being the rule, is the exception.

This want of agreement among those who have given the subject most attention makes the determination of the actual method of gastrulation in Aurelia a matter of considerable interest, and it may be assumed that any contribution to the solution of the question will not be unwelcome.

Early in the current year, at the suggestion of Dr. E. L. Mark, I undertook to investigate the method of gastrulation in A. flavidula.

Through the kindness of Mr. B. H. Van Vleck of the Boston Society of Natural History, I was enabled to spend two months of the summer of 1887 at his seaside Laboratory at Annisquam, Mass., where I then collected the material used in the present study. The embryos were killed with picro-nitric acid, and preserved in 90 per cent alcohol, in which they have been kept during the three intervening years. Of the various staining fluids tried, Erlich's acid hæmatoxylin gave decidedly the best results for sections. For examination of the whole embryos, Grenacher's alcoholic borax-carmine and Czokor's alum-cochineal each gave good results. The latter stain possesses the peculiarity of staining embryos of different ages with corresponding degrees of intensity, the youngest stages being stained the least, the degree of intensity increasing with the age of the embryo up to the planula stage.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXIX.

The result of segmentation is a one-layered blastosphere, as in A. aurita. Although the diameter of the blastocœl, or segmentation cavity, presents some individual variations at a given stage of development, it in general corresponds very nearly with that of A. aurita, as described by Goette ('87, p. 3). It increases slightly as the process of gastrulation advances. The cells of the blastosphere are usually somewhat shorter at one pole than elsewhere, and it is from this region that the entoderm is formed. The nuclei of all the cells are situated very near the outer surface of the blastosphere. Small spheroidal bodies constitute the greater portion of each cell; they are very evenly distributed through its substance, except in the vicinity of the nucleus, where they are somewhat less abundant. Vacuoles of variable sizes are usually found in some of the cells. The nuclear region stains a little more deeply than the remaining portion.

The method of gastrulation in A. flavidula is similar to that in A. aurita as described by Claus ('83, pp. 2 and 3), although it resembles even more closely a typical invagination. When the process of cleavage has resulted in the formation of a blastosphere composed of somewhat more than four hundred cells, a depression of limited extent appears in the portion of the wall which is composed of the shorter cells. From this depressed region is formed the entoderm, which develops as a single continuous layer of cells surrounding a small cavity, the cœlenteron. At the beginning of the process, and throughout its duration, the cœlenteron is in communication with the exterior by means of a narrow passage, the blastopore, or blastoporic canal. See also Explanation of Figures (Plate I. Figs. 1–4). From these figures it is apparent that only a small portion of the wall of the blastosphere is concerned in the invagination, and to that extent it must be regarded as deviating from the typical invagination, where one half of the wall of the blastosphere is infolded to form the entoderm. The cœlenteron is, however, at all stages of gastrulation, an open sac-like cavity, and therefore noticeably different from that of A. aurita, of which Claus ('83, p. 3), says: "Mit dem weiteren Nachrücken der die Mundspalte begrenzenden Zellen in das Innere des

Larvenleibes ändert sich jedoch allmählig das frühere Verhältniss zu Gunsten der Entodermfüllung, *die noch immer keine wahre Höhle, sondern eine schmale lineare, mit der Hauptachse des Leibes zusammenfallende Spalte besitzt.*"[1] With the growth of the entodermal layer, the cœlenteron enlarges, and the cleavage cavity is diminished, until finally it is entirely obliterated and the entoderm everywhere comes into contact with the ectoderm (Plate I. Figs. 4–6, Plate II. Fig. 11).

During the process of gastrulation, and also for a short time after its completion, the thickness of the entoderm, which is much less than that of the ectoderm, does not increase. Figures 5 and 6 (Plate I.) are from sections of two embryos at different stages of development. Figure 5 is from an embryo soon after the completion of gastrulation; Figure 6 is from an older stage. Since in each case the section is from the middle of its series, it follows that a decided thickening of the entoderm takes place between the stages represented by these Figures. This thickening is apparently due to an increase in the number of the cells, which are soon unable to find room for themselves except by elongation. The entodermal cells are quite different in appearance from those of the ectoderm; they are approximately spherical, and do not have as numerous spheroidal yolk bodies as the latter. Their nuclei, however, closely resemble those of the ectoderm, and usually lie in the portion of the cell nearest the cœlenteron.

As is to be seen from Plate II. Fig. 7, — a section nearly perpendicular to the blastoporic canal, — the blastopore in A. flavidula is very small. A similar condition has been shown by Claus to exist in A. aurita, and by Metschnikoff ('86, Taf. X. Fig. 14) in Nausithoë marginata.

The nuclei of the cells composing the wall of the blastosphere are situated, as has been stated, near the surface of the sphere. But at about the time of the beginning of the invagination, sometimes a little earlier, a few of the nuclei are found in the deeper portion of the wall. At first there are only one or two such displaced nuclei to be observed in the whole embryo, but as development progresses they increase in number. A careful examination of sections shows that the cells to which they belong do not extend, like the remaining cells of the wall, through its whole thickness, but that they are wedged in as it were between the bases of the ordinary cells. The latter are much elongated, and from mutual pressure are prismatic, whereas the deep cells are spheroidal and project in some cases into the segmentation cavity. Since these cells are found at various intermediate positions between the outer and inner surfaces of the wall, I infer that they result from a process of migration inward, either at the time of cell division or independently of that process. Indeed, there is obviously no other possible source whence these cells could come, but the exact process of transfer is not easily determined. I believe that this increase in number is at first for a considerable time due exclusively to the migration of cells which once shared in forming the external boundary of the sphere, but later the division of cells which have already migrated into the deeper portion of the ectoderm undoubtedly contributes to this increase.

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[1] The original is not Italicized.

We have now to turn our attention to a phenomenon of considerable importance, the study of which from preserved material is, however, attended with difficulties. I refer to the ingression of cells from the wall of the blastosphere into the cleavage cavity, which begins a considerable time before the invagination commences. The latter does not take place until the number of cells forming the wall of the blastosphere has exceeded 400, whereas the ingression, as far as can be inferred from the cases which I have studied, may occur at any time after the blastosphere contains about 100 cells up to the period of invagination. The phenomenon of ingression in A. flavidula is not of constant occurrence, but when it does take place is similar to that represented by Goette ('87, Taf. I. Figs. 1–5) for the earlier stages of the blastula in A. aurita. It consists of a migration into the cleavage cavity of one or two, rarely more than three, of the cells of the blastospheric wall. With the exception that they assume a spherical form, because relieved from pressure, they are at first similar in size, as well as in nuclear and other characters, to the cells remaining in the wall.

The study of ingression upon preserved material is attended with difficulty, since in any one specimen we have the condition at only one stage of development, and cannot say with certainty what its condition has been in past stages, or what it might have been during some subsequent period. This can be determined only by studying the conditions existing in other embryos killed at other stages, and arranging all in their probable natural sequence. In view of this fact, I have sectioned and examined several hundred embryos which were killed at different stages of development. As far as possible the results obtained from these sections have been verified by the study of embryos cleared and mounted whole. Although this ingression occurs before invagination, I have deferred the discussion of it until now, because invagination is constant in its occurrence, whereas the ingression does not appear to be so; indeed, the majority of the specimens have shown no indications of it.

The subsequent history of these cells, as shown by the comparison of specimens of succeeding stages of development is both interesting and peculiar. I imagine that it is such cells as these to which Claus ('90, p. 3) refers when he says : "Ich habe den vereinzelt eingetretenen zwei bis drei Zellen, weil sie nicht regelmässig in jeder Blastula sich ablösen, der am vegetativen Pole einwuchernden Zellenmasse gegenüber keine weitere Bedeutung beigemessen, so dasse ich dieselben zwar auf einer Abbildung darstellte, im Texte aber nicht besonders erwähnte, und bin auch jetzt noch der Ansicht, dass diese auffallend kleinen Zellen wieder rückgebildet werden und überhaupt nicht zur Bildung des Entoderms beitragen." In my judgment, a part of the difference of opinion between Goette and Claus is due to the fact that there are two kinds of cells which find their way into the cleavage cavity. These are the large cells described by Goette as beginning to be formed at an early stage of the blastula, and much smaller cells, of which I shall have more to say hereafter, that make their appearance only at later stages of development. Claus seems to have seen "very small cells," and to have assumed that they were equivalent to the large cells figured by Goette. I am unable to say with certainty that the cells seen by Claus are the equivalents of those figured by Goette, but Claus assumes that they are, and I have the more reason to believe it because the large cells are of more frequent occurrence than the small ones. But if this be so, I do not understand how Claus could speak of them as "diese auffallend kleinen Zellen." But however that may be, I have reason to believe that the supposition of Claus, that they ultimately degenerate, is correct.

Soon after the ingression of a cell its nucleus undergoes changes which result in its disappearance as such, for instead of a nucleus there can be seen only one or more small, isolated, deeply stained particles, which I judge to be scattered portions of the nuclear chromatine (Plate II. Figs. 8 and 10). Even these are often wanting. I have said that this nuclear change follows soon after the ingression of the cell, because out of the numerous instances in which these cells have been present there is not one in which the nucleus retains its original condition after the cells in the wall of the blastula have given evidence, by their diminished size, that they have undergone division since the ingression took place. This conclusion is in part based on the assumption that at the time of ingression the ingressing cells are of about the same size as those which remain in the wall of the blastula. The ingressing cells sometimes persist, without any further apparent changes than the disintegration of the nucleus, until the process of gastrulation is completed. Such cases are not as common, however, as others, where there is to be found in the cleavage cavity material which appears as though it had resulted from the disintegration of similar cells. This material has a spongy or vacuolated appearance, and contains faintly staining bodies or granules similar to those found in the ectodermic cells; it does not possess definitely circumscribed boundaries; on the contrary, it fills the cleavage cavity more or less completely, but is not of uniform density throughout. The fact that this material is not homogeneous, and that it contains granules, etc., prevents the conclusion that it has been produced as a simple secretion into the cleavage cavity, although it may have been formed in part by such a process. The frequent association of this material with ingression cells in the same specimen (Plate II. Fig. 8), and the lack of other ways of accounting for its presence, lead me to believe that it is produced by the disintegration which I have suggested.

There is another peculiarity of the development which I believe to be connected with this process of nuclear disintegration. It is this: after having once entered the cleavage cavity the immigrating cells seem to lose their power of division, and consequently do not become more numerous, while the cells composing the blastospheric wall undergo repeated divisions, as is shown by their increased number and diminished size.

The number of these immigrating cells is small, usually only one or two, very rarely more than three, so that I have not been successful in finding the "Verbindungsglieder" connecting the conditions shown by Goette ('87, Taf. I.) in his Figures 5 and 6, which Claus ('90, p. 4) regarded as essential to the substantiation of Goette's view of the method of gastrulation.

Reference has been made to the fact that in some cases the ingrowing cells persist both during and after the process of invagination. In the latter case, they are to be found in the cœlenteron rather than in the cleavage cavity. Figure 11 (Plate II.) is drawn from such a specimen. Figures 9 and 10 represent two sections of one individual in which the invagination is not completed, and furnish a hint as to the process by which the cells pass into the cœlenteron from the cleavage cavity. The entoderm being composed of less closely fitting cells than the ectoderm, doubtless admits the passage of the large immigrated cells through it more readily than the latter would (Plate II. Fig. 9). The immigrated cell is of course passive in this process. Since it is prevented by the firm wall of the ectoderm from escaping, the pressure exerted upon it by the enlarging entoderm is probably sufficient to cause it to be forced through the entodermic wall into the cœlenteric cavity. From Figure 10 it is to be seen that one cell has already reached the gastral cavity. In speaking of these peculiarly situated cells I have thus far assumed that they are such as originally reached the cleavage cavity by an early ingression, where, with changed nuclear condition, but apparently with no further alteration, they have remained until the time of gastrulation. That this is their source is evident from the following considerations. First, the small diameter of the blastoporic canal (Plate II. Fig. 7), which is from the same series as Figures 9 and 10, precludes the assumption that they might have entered the gastrula cavity from without. Secondly, in their large size and general appearance they are unlike the cells of either ectoderm or entoderm at any time during gastrulation, and so could not have been derived from those sources during that process. Thirdly, they do correspond in size and general characters, except in their nuclear conditions, with the cells of the blastospheric wall as the latter appear at the time when ingression takes place.

It is difficult to state either the cause or the purpose of this immigration. That it is not essential to the welfare of the embryo, either by affording nourishment to the developing cells of the entoderm, or in any other way, is evident from the fact that in a large number of cases it does not occur. That it is not an inherited tendency, derived from a more primitive method of gastrulation by ingression, is probable from the fact that the immigrating cells do not appear to have any share whatever in the formation of the entoderm. On the other hand, its occurrence seems to be much too frequent to be considered as accidental.

I have stated previously (p. 119) that two very different kinds of cells are to be found at times in the cleavage cavity. Besides the large immigrating cells already described at length, I have found in a much smaller number of cases very small cells (Plate I. Fig. 2), one or two in number, that appear precisely like the deep-lying ectodermal cells already described. Because of their strong resemblance to the latter, their exceptional occurrence, and the fact that they do not appear until after the beginning of the development of the deep-lying ectodermal layer, I incline to the opinion that they are derived from that layer, and that their occurrence is entirely accidental.

At first it appeared to me surprising that two investigators could reach such different conclusions as those published by Claus ('83 and '90) and Goette ('87), concerning the method of gastrulation in the same animal, A. aurita. Since studying this process in A. flavidula, it seems less strange. The results obtained from my first sections led me to think that the conclusions reached by Goette would be confirmed in the case of A. flavidula. Better staining, thinner sections, and more accurate orientation have made it certain, however, that the method of gastrulation in this species is much more in accord with the description given by Claus, and that the process really is one of invagination.

Certain considerations weaken my confidence in the position defended by Goette. A comparison of his Figures 6–9 ('87, Taf. I.) with some of my thicker sections, or with those which were made when the gastrula was so oriented as not to be cut parallel to the blastoporic canal, makes it appear to me probable that his results are based upon similar inadequate sections. In Figure 8 (Plate II.) there are only about one half as many nuclei visible as there are cells, the nuclei of a portion of the cells being contained in adjacent sections. In figures of corresponding stages of A. aurita as represented by Goette ('87, Taf. I.), nuclei are figured in *nearly all the cells.* I believe this to be evidence that his figures were drawn from *thick* sections. The blastopore, because of its very small diameter, is quite easily overlooked in thick sections, and especially if the plane of sectioning is somewhat oblique to the longitudinal axis of the blastopore. Since, as previously stated, the nuclei of the entodermal cells are usually situated in the portion of the cell nearest the cœlenteron, it is easy to find in thick sections of an invaginating embryo conditions like those represented by Goette in his Figures 6–8. My Figure 12 (Plate II.) reproduces a section of the same series as that represented in Figure 3 (Plate I.). The intervening section (not figured) is quite similar to Goette's Figure 8. An examination of the cells bordering the blastoporic canal in Figure 3 will show how sections like Figure 12, or such as are a little oblique to the chief axis of the embryo have the appearance of containing immigrating cells. Such sections also exhibit the flattening in the region of the shorter cells to which Goette ('87, p. 4) has called attention in the following words: "Schon während der Gastrulation zeigt sich eine Stelle des Keims im Bereich seiner kürzeren Zellen etwas abgeplattet."

Additional considerations increase the probability of the correctness of the view which I have advanced to explain Goette's error. With advancing stages of development, I have found an increase in the number of the cells composing the ectodermic wall. This is undoubtedly subject to slight individual variations, but the number of such cells is nevertheless in quite close correlation with the stage of development. An examination of Goette's Figures 6–9 ('87, Taf. I.) reveals such a similarity in the number and size of the cells composing the ectoderm in each of the four supposed stages, that I am driven to the conclusion that they represent sections from specimens of a single stage of development, which may have been produced by cutting in planes having different relations to the chief axis of the embryo.

When we consider that in the majority of embryos there are no signs of ingression, and that in the cases where it does occur the immigrating cells in some instances degenerate early, and in others persist undivided throughout the process of gastrulation, and that they at no time show evidences of even sharing in the formation of an entoderm, — and when we further reflect that all the conditions shown in Goette's Figures 6–9 can easily be reproduced from sections of invaginating gastrulæ of a single stage of development, — it seems improbable that the entoderm of Aurelia develops even occasionally by ingression. At present, therefore, there seems to me to be no evidence that in this genus gastrulation occurs by both methods, invagination and ingression.

The Scyphomedusæ present several interesting variations in gastrulation. The anomalous development occurring in Lucernaria is as far removed from the usual process as that group itself is from the other Scyphomedusæ. According to McMurrich ('91, p. 314), the solid planula in Cyanea arctica is formed by the immigration of certain of the blastula cells. This planula is subsequently hollowed out, and gives rise to a structure like an invaginate gastrula, but it is formed without any invagination. In Cyanea capillata (Hamann, '90, pp. 16, 17) there seems to be a solid ingrowth of cells from one pole of the embryo, and a simultaneous development of the cœlenteron. The entoderm of Chrysaora (Claus, '83, p. 5, Taf. I. Fig. 21 *h*) is developed in a way which is somewhat similar to that described by Hamann for Cyanea capillata. According to Claus ('83, p. 2, and '90, p. 4), the gastrulation of Aurelia aurita approximates the method by invagination a little more closely than that of Chrysaora, since its cells are arranged in a single layer about the fissure-like cœlenteron. Aurelia flavidula exhibits a still more nearly typical invagination, since the cœlenteron is from the beginning an open sac-like cavity. Cotylorhiza tuberculata (Cassiopea Borbonica) has an invaginate gastrula which closely resembles that of Aurelia flavidula (Claus, '90, Taf. I. Figs. 2 and 3; Kowalevsky, '73, Taf. II. Fig. 1). Finally, in Pelagia noctiluca and Nausithoë marginata, as shown by Metschnikoff ('86, pp. 66–68, Taf. X.), there is a typical invagination.

If the observations of McMurrich ('91, p. 314) on Cyanea arctica are substantiated, we have among the Scyphomedusæ one example of the formation of a sterrula by ingression, with the subsequent formation of a gastrula-like structure, without an invagination. From the preceding summary it is to be seen that there are in Scyphomedusæ two cases in which the mode of gastrulation appears to be intermediate between ingression and invagination, and at least four cases of unquestionable invagination. If, in the light of so much variation in the mode of gastrulation in this group as is shown by the few forms studied, it is safe to conclude that any one mode is typical, that mode would certainly appear to be invagination, and not, as Hamann and McMurrich have recently maintained, ingression.

Cambridge, June 20, 1891.

BIBLIOGRAPHY.

Claus, C.

'83. Untersuchungen über die Organization und Entwicklung der Medusen. Prag u. Leipzig, 96 pp.

'90. Ueber die Entwicklung des Scyphostoma von Cotylorhiza, Aurelia und Chrysaora, sowie über die systematische Stellung der Scyphomedusen. I. Arbeiten a. d. zool. Inst. Wien, Tom. IX. p. 85.

Goette, A.

'87. Abhandlungen zur Entwicklungsgeschichte der Tiere. Viertes Heft. Entwicklungsgeschichte der Aurelia aurita und Cotylorhiza tuberculata. Hamburg u. Leipzig, 79 pp.

Hamann, O.

'90. Ueber die Entstehung der Keimblätter. Ein Erklärungsversuch. Internat. Monatsschr. f. Anat. u. Physiol., Bd. VII. pp. 1–28.

Kowalevsky, A.

'73. Untersuchungen über die Entwicklung der Coelenteraten. Nachrichten Gesellsch. Freunde Naturerkennt., Anthropol. u. Ethnog. Moskau, 1873. (Russian.)

See also Hoffmann u. Schwalbe, Jahresbericht, Bd. II. p. 279.

McMurrich, J. P.

'91. Contributions on the Morphology of the Actinozoa. II. On the Development of the Hexactiniæ. Jour. Morphol., Vol. IV. p. 303.

'91^a. The Gastræa Theory and its Successors. Biological Lectures delivered at the Marine Biol. Laboratory, Wood's Holl. Boston, p. 79.

Metschnikoff, E.

'86. Embryologischestudien an Medusen. Wien, 159 pp.

EXPLANATION OF FIGURES.

All the figures were drawn from sections with the aid of an Abbé camera. The sections from which the figures were made were 5 μ in thickness.

PLATE I.

ABBREVIATIONS.

bl'po.	Blastopore.
cav. sg.	Segmentation cavity.
cl.	Immigrated cell.
cœlent.	Cœlenteron.
cog.	Coagulum.
ec'drm.	Ectoderm.
en'drm.	Entoderm.
nl.	Chromatic portion of degenerated nucleus.
nl. ec'drm.	Nuclei of deeper portion of ectoderm.

Figures 1–4. Sections to illustrate the nature of the invagination.

Fig. 1. An early stage of invagination. × 460.

" 2. A slightly later stage than that of Figure 1. × 540.

" 3. A stage in which the invagination is well advanced. × 385.

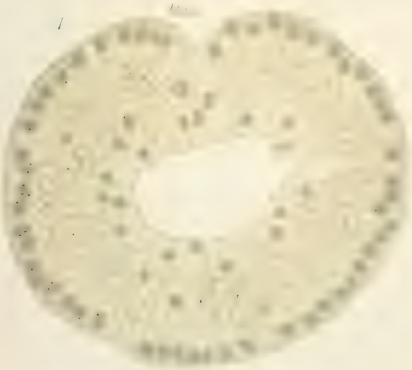
" 4. A gastrula with invagination completed. × 410.

" 5. Section of a gastrula cut in a plane (equator) perpendicular to the axis of the blastoporic canal. × 385.

" 6. Section of an older individual through the equator, showing increase in thickness of the entoderm. × 385.

SMITH.—GASTRULATION IN AURELIA.

1



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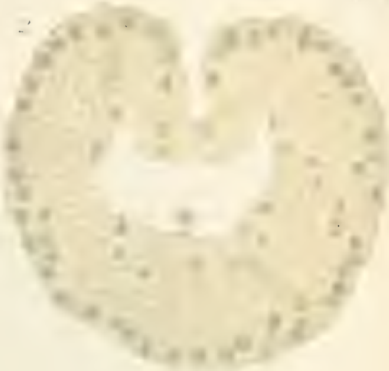

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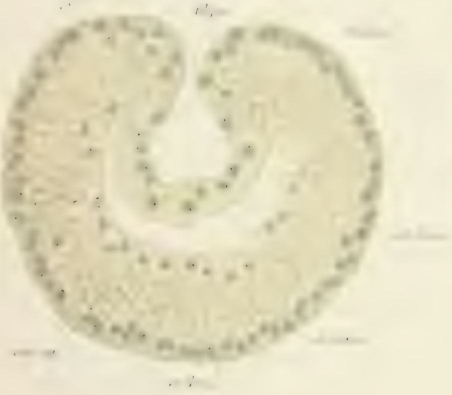

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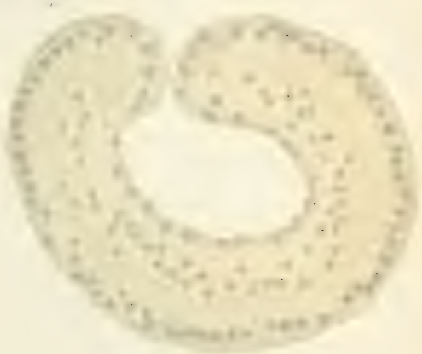

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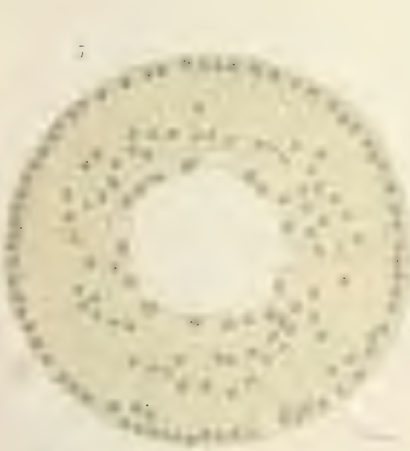

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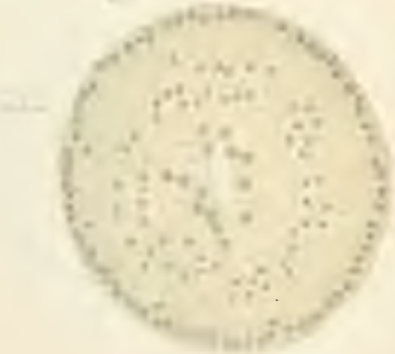


B. Meisel, lith. Boston.

PLATE II.

ABBREVIATIONS.

bl'po.	Blastopore.
cav. sg.	Segmentation cavity.
cl.	Immigrated cell.
cœlent.	Cœlenteron.
cog.	Coagulum.
ec'drm.	Ectoderm.
en'drm.	Entoderm.
nl.	Chromatic portion of degenerated nucleus.
nl. ec'drm.	Nuclei of deeper portion of ectoderm.

Figures 7, 9, and 10 are from different sections of the same individual.

Fig. 7. Section through the blastoporic canal and nearly perpendicular to it. × 410.

" 8. Section at a stage preceding invagination. It shows an immigrated cell in which the nucleus has degenerated. × 385.

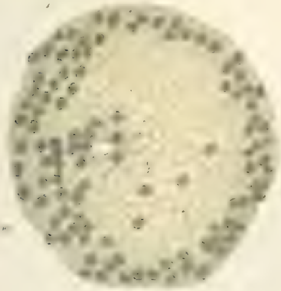
" 9. Section before the close of gastrulation, showing an immigrated cell in the segmentation cavity. × 410.

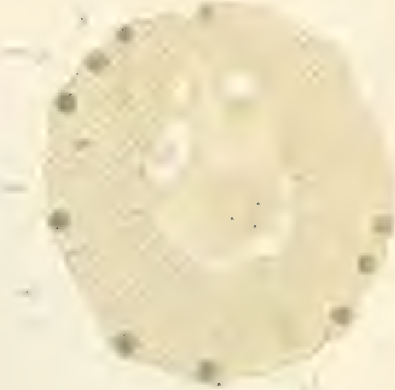
" 10. Section from the same individual as Figure 9. It contains an immigrated cell in the cœlenteric cavity. × 410.

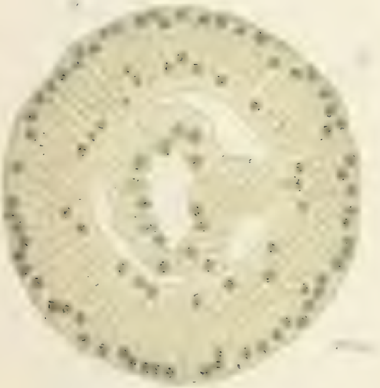
" 11. Section of a gastrula with two immigrated cells contained in the cœlenteric cavity. × 385.

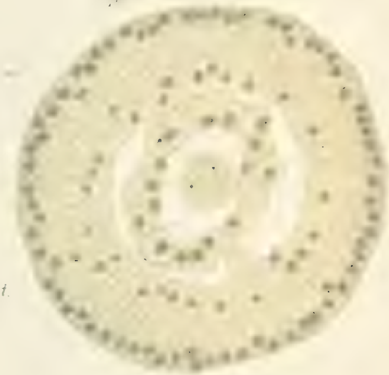
" 12. Section from the same individual as Figure 3, to show the appearance when the gastrula is cut parallel to, but at one side of, the blastoporic canal. × 385.

7









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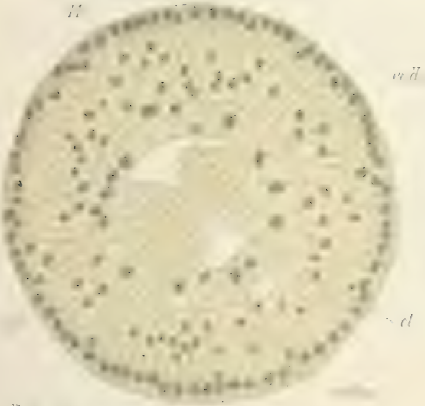

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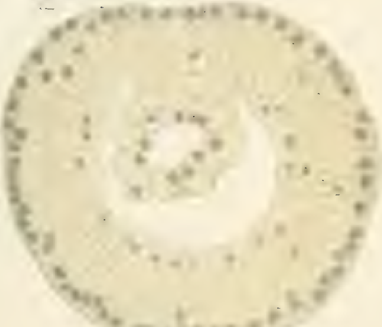

No. 3. — *Amitosis in the Embryonal Envelopes of the Scorpion.*

By H. P. Johnson.[1]

In the fall of 1889, at the suggestion of my instructor, Prof. E. L. Mark, I decided to work upon the problem of the so-called "direct" or amitotic division of nuclei. While in search of suitable material, my attention was called to a brief article by Blochmann ('85), describing a very well marked amitotic division for the large nuclei of the embryonal membrane of the scorpion. A number of *Centrurus* embryos were kindly given to me by my friend, Dr. G. H. Parker. These embryos had lain in 90% alcohol since the summer of 1886. The mode of fixation (for the purpose of studying the development of the eyes) was somewhat unusual; for, immediately after their removal from the mother, they were immersed in 35% alcohol, and thence carried up quite rapidly, through 50 and 70%, to 90%. Notwithstanding this rather crude method, the membranes were in excellent histological condition, in no way inferior to material afterwards prepared by the most approved methods of fixation.

In addition to the material above mentioned, I received from Mr. Richard Goeth, of Burnet County, Texas, during the following winter and spring, about three dozen live specimens of *Centrurus* (sp. incog.).[2] A lot that arrived in the latter part of May contained several pregnant females, with embryos in different stages. The scorpions were chloroformed, and the ovarian tubes with the embryos enclosed were dissected out as quickly as possible. A number of killing agents were used, including Flemming's weaker chrom-aceto-osmic, Rabl's chrom-formic, Perenyi's fluid, Kleinenberg's picro-sulphuric, and Merkel's fluid.

For staining, I have used chiefly Ehrlich's hæmatoxylin. Grenacher's alcoholic borax-carmine and Czokor's alum-cochineal have given fair results. Safranin, employed according to Flemming's method, I have found less serviceable than the stains above mentioned. After staining, the preparations were dehydrated, cleared with oil of cloves, and mounted in benzole-balsam.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy, under the direction of E. L. Mark, No. XXX.

[2] This is the species used by G. H. Parker in his study on the development of the eyes (see Bull. Mus. Comp. Zoöl., Vol. XIII. No. 6, p. 173, 1887), and was then undescribed. I am not aware that it has since received a name.

The embryo is enveloped by three epithelial membranes, the ovarian capsule, the *membrana serosa*, and the amnion, — named in order from without inward.

The serosa and amnion are strictly embryonic structures, analogous to the fœtal membranes of the higher Vertebrates. There are two contradictory accounts as to the manner of their formation. Possibly they do not arise in the same way in all genera of scorpions. In a brief communication by Kowalevsky und Schulgin ('86, p. 526) upon the development of *Androctonus ornatus*, it is stated that they originate as a fold from the edge of the blastoderm, the outer layer of the fold forming the serosa, the inner the amnion. The fold grows up over the blastoderm, the edges coalesce, and the membranes finally separate from the ovum. The more recent account by Laurie ('90, p. 114) states that in *Euscorpius* the serosa arises by a proliferation of the peripheral cells of the blastoderm, extends as a delicate membrane forward and backward over the egg, which it finally covers completely, and then becomes entirely separate from the blastoderm. The formation of the amnion begins when the serosa has covered about two thirds of the embryo, and, like the serosa, its origin is ectodermic. The amnion, however, "never loses its connection with the epiblast as the serous membrane has now done, but remains attached to its edges and only extends round the egg as the epiblast extends" (p. 116). Unfortunately, I have not obtained sufficiently early stages of *Centrurus* to ascertain how its membranes arise, but, in removing the latter from the embryo, I have never found the amnion attached to the ectoderm. The membrane which I have called the "ovarian capsule" I at first wrongly took to be the follicular epithelium, and under this supposition it was indicated as *e'th. fol.* in Figure 2. Like the follicular epithelium, it arises from the ovarian tube; but the follicle is formed as a diverticulum of the tube, previous to the maturation of the ovum, and serves as a nutritive capsule for the latter during its growth. The ovarian capsule, on the contrary, is that part of the ovarian tube which receives the ovum after fertilization, and enlarges to accommodate the growth of the embryo.

The fœtal membranes fit so loosely over the embryo that they can be easily removed in a single piece. In late stages, the ovarian capsule is readily separable from the membranes; in earlier stages, it adheres closely to them. It is rarely possible to separate the serosa from the amnion, and a transverse section (see Fig. 2) shows only a trace of a dividing wall between them, although in surface view the cell walls of both membranes are clearly seen (Fig. 1). Metschnikoff (71, p. 219) describes the membranes of *Scorpio* (*Euscorpius*) *italicus* as connected with each other by delicate fibres, which terminate just over the amniotic nuclei. I have found such fibres in the earlier stages of my material, but not in the older ones, nor are they everywhere present in the younger membranes. The membranes of the Brazilian scorpion examined by Blochmann ('85, p. 481) were found closely applied to each other.

I. The Serosa.

Plate I.; Plate II. Figs. 14, 15; Plate III.

The cells of the serosa have great superficial extent, measuring half a millimeter or more in diameter; but proportionally they are very thin. Their size is exceedingly variable, as may be seen by comparing Figure 3 with Figures 11 and 13 of the same magnification, although the last two represent cells of only average size. Both small and large cells are apt to be aggregated in certain parts of the serosa, yet very small cells often occur sporadically in the midst of large ones. The cell walls are extremely distinct in late stages of the embryo, but in earlier stages are often difficult to trace in an ordinary stained preparation. As remarked by Blochmann, they have a distinct fibrous structure. The cells are irregularly polygonal in shape, usually elongated, sometimes nearly square or triangular. Not infrequently they are bounded by curved outlines (Fig. 13).

The nuclei of the serosa measure from $25\,\mu$ to $60\,\mu$ or more in diameter, but as a rule are small in proportion to the cells (Figs. 1–3 and 11–15). In the membranes of young embryos the nuclei are larger absolutely and in proportion to the cells than in old membranes. In face view the resting nucleus is nearly circular; in section, it is seen to be considerably flattened, in accordance with the thinness of the cell (Fig. 2, *nl. sr.*). It occupies the full thickness of the serosa, and sometimes causes a bulging of the cell at the point where it lies, as is shown in Figure 2. Blochmann states ('85, p. 480) that the nuclei of the serosa always cause that membrane to encroach *inward* upon the amnion; but a dividing line between amnion and serosa is so seldom visible in *Centrurus*, that I am unable to say whether such is the case.

The nuclear membrane is thin, but clearly visible, except in nuclei that have undergone degeneration. The chromatic substance, or nuclein, is for the most part in the form of granules distributed evenly throughout the nucleus. Indications of a reticular or filamentous structure are, however, frequently present. I believe there is a chromatic network throughout the nucleus, but the abundance of granular chromatin prevents one from tracing it. Several nucleoli are always present. They are extremely variable in size and shape, and in many cases appear to be only aggregations of granular chromatin. They take a stain with hæmatoxylin and carmine in no way different from the rest of the chromatin, except that it is more intense.

A very large proportion (about four to one) of the cells of the serosa contain two nuclei. These pairs of nuclei have all arisen from single nuclei by amitotic division. It is obvious that division of the cell is not contemporaneous with, and does not immediately follow, the division of the nucleus. In many cases, especially when the embryo is far advanced, cell division probably does not occur at all. Very few cells out of the thousands I have examined have had more than two nuclei; but I have found several with three nuclei, and two cells with *four*. This seems to be the maximum number. These cells of the serosa, therefore, are not to be classed with multinucleate cells in which the nucleus divides into a great number of irregular and unequal fragments. Here the division takes place in an orderly fashion, and division of the cell follows nuclear division in regular sequence, though not immediately.

In every serosa examined, nuclei were found in process of division. Some preparations furnish many more examples of division than others; and occasionally three or four adjacent cells will contain dividing nuclei (Fig. 15). Very frequently, however, only one or two dividing nuclei will be found in the whole serosa. It cannot therefore be supposed that nuclear division is frequent; and I have found that there are more cells with dividing nuclei in the membranes of late stages of the embryo than in the earlier ones.

The first sign of approaching division is an elongation of the nucleus (Fig. 4), almost always parallel to the long axis of the cell. Naturally, the elongation progresses by insensible gradations from the nearly circular form of the resting nucleus, so that one cannot say positively that the nucleus is going to divide until the elongation has become marked. The absolute amount of elongation varies greatly, and is less in the membranes of young embryos than in those of older ones. The example represented in Figure 4 is from an old membrane, and shows almost the extreme of elongation. This stage, while giving not the slightest evidence of ordinary mitosis, is characterized by a longitudinal arrangement of the chromatic substance, as indicated in Figure 4. The effect is most marked upon the nucleoli. Blochmann ('85, p. 482) found only two nucleoli at this stage, and these were usually situated one at each end of the elliptical nucleus. Where there are several nucleoli, as is usually the case with the nuclei I have studied, there is an approximately equal distribution of them to the daughter nuclei. The nucleoli vary so much in size and shape, that it is impossible to say how precise is the apportionment of chromatin by this method.

Most nuclei in the elongated condition already show a slight constriction, generally more marked on one edge than on the other (Fig. 4). If no further elongation takes place, the constriction becomes deep and narrow, as represented in Figures 5 and 12. This style of division is characteristic of young membranes, and gives rise to daughter nuclei which lie close together, or even in contact (Fig. 13). It is doubtless a more vigorous and rapid type of division than that found in the older membranes, to be described directly. If the nucleus continues to elongate while constricting, it assumes the dumb-bell form represented in Figures 6 and 7. The daughter nuclei, at first ovate or pyriform, become rounder as the connecting thread becomes thinner. Division of this type is almost confined to old membranes; I have rarely found it in those from young embryos.

The nuclei represented by Figures 6 and 7 show more clearly than usual a peculiar arrangement of the chromatic threads. The filaments have the appearance of a fascicle of slender rods, which lie very close together in the connecting bridge, and thence radiate into both daughter nuclei. They are stainable both with carmine and hæmatoxylin. Sometimes these threads can be resolved into rows of granules (Fig. 7, right-hand daughter nucleus). The later stages also show traces of these longitudinal threads (Figs. 8, 9, 10). In the example represented by Figure 6, the nucleoli partook of the general longitudinal disposition of the chromatic substance, but were probably arranged in this manner at an earlier stage of division, as explained for Figure 4. In the later stages of division, this arrangement of the nucleoli is gradually lost.

The final stages, represented in Figures 8, 9, 10, may be briefly described. These stages are far commoner than the early ones; hence, it must be supposed that they require more time. The constricted portion is drawn out into a thin, deeply staining thread. This thread undoubtedly contains chromatin, and in a peculiarly condensed form. In this respect these nuclei differ from the nuclei of the Malpighian vessels of *Aphrophora spumaria*, as described and figured by Carnoy

('85, Plate I. Fig. 7); for the connecting thread in the dividing nucleus of *Aphrophora* remains unstained, and therefore contains no chromatin.

The dividing nucleus represented by Figure 8 is peculiar in several respects. In the first place, the daughter nuclei are very unlike in form, though this is by no means unusual with dividing nuclei from old membranes. All the stainable nucleoli are in one daughter nucleus, while the other still shows a faint longitudinal arrangement of its chromatic threads. The sharply stained connecting thread is notched at a point midway between the daughter nuclei, probably indicating the place where, at a later stage, rupture would have occurred. The daughter nucleus on the left is nearly destitute of chromatin in the crescent-shaped space lying next the connecting thread, and an inner contour line is visible (x), from the central point of which a stainable cord extends to the proximal end of the connecting thread. I have seen a similar appearance in the late stages of other dividing nuclei, and it undoubtedly indicates the manner in which the daughter nuclei sometimes attain a rounded form. Occasionally, however, daughter nuclei entirely separate from each other have a conical or tapered form.

In the last stages of division, the connecting thread is drawn out to extreme tenuity (Figs. 9 and 10). So exceedingly fine does this thread become, that, with the highest power accessible to me (Zeiss's homogeneous immersion objective $\frac{1}{18}$), I could barely trace its course through the cytoplasm, though in most cases I made out that it was continuous from nucleus to nucleus. It is finally broken at or near the centre, and the proximal tips, as Blochmann suggests, are probably absorbed by the daughter nuclei. In even so late a stage as that shown by Figure 10, the longitudinal chromatic filaments are still perceptible. The right-hand daughter nucleus contains four loop-shaped bodies that strongly resemble chromosomes. They are, however, almost unstained by hæmatoxylin.

Blochmann states ('85, p. 482) that in no case did he find a division of the cell following the division of the nucleus. As already said, the great proportion of binucleate cells renders it certain that cell division is not an *immediate* consequence of nuclear division. Although I have carefully examined great numbers of binucleate cells, I have only once seen a cell wall in process of formation (Fig. 27). Yet one finds plenty of evidence that cell division does take place. Pairs of cells like those in Figure 11 are of frequent occurrence. It is safe to infer, I think, from the arrangement of the binucleate cells which surround these, as well as from the correspondence in size and shape of this pair, that they have arisen from an elongated binucleate cell by the formation of a divisional cell wall. In one instance, I have found a cell wall *fully formed before division of the nucleus was completed* (Fig. 27). It cuts across the fine connecting thread at about the middle point of the latter. This must be considered as in some degree abnormal, especially since it was found in a serosa the nuclei of which had evidently degenerated.

Although division of the cell is almost always accomplished by the formation of a cell wall, I have found several *constricted cells,* showing that division may be partly, or even wholly, effected in this manner. Sometimes the constriction is so deep that the opposite walls meet (Fig. 28); but it is more usual to find that, after the cell has become considerably constricted, a cell wall is formed joining the inward curves of the constriction, and completing the division. At first, I thought it possible that the constriction was mechanically produced by the pressure of growing cells on either side. But this would not explain the invariable occurrence of the constriction at precisely the point where it would take place in a free cell, — equidistant from the daughter nuclei. Furthermore, the curvature of cell walls (see Fig. 13), which is almost certainly caused by the growth of cells and consequent tension, has no reference to the position of the nuclei.

As far as can be judged, the daughter nuclei are, as a rule, of equal size, and alike in shape. I have found many instances of beautifully symmetrical division (Figs. 9 and 10); but the nuclei of the serosa are not altogether exempt from the irregularities that seem to be inseparable from amitotic division wherever it occurs. Sometimes the resulting nuclei are obviously unequal (Fig. 13), even in young membranes; and in old membranes, where the nuclei have undergone degeneration, not only are the daughter nuclei extremely irregular in shape, but often very dissimilar in size.

Relations of the Nuclei to the Cell. — A very brief examination of a preparation of the serosa convinces one that the nuclei are symmetrically arranged in the cells. When there is but one nucleus, it occupies the centre of the cell; when there are two or three nuclei, each presides over a half or a third of the cytoplasm. This arrangement is so constant, that any marked deviation from it catches the eye at once. Instances of decidedly unsymmetrical arrangement of nuclei, one of which Figure 13 represents, are very unusual. As regards elongated cells, the daughter nuclei lie in the *long axis* of the cell, and at approximately equal distances from its ends. Occasionally, however, the nuclei lie in the *short axis* (Fig. 12), and much more frequently are placed *obliquely*, as in cell *a*, Figure 14. We would suppose that, in the event of division of an elongated cell with nuclei lying transversely, the cell wall would pass longitudinally between the nuclei; but I have not been able to find evidence of longitudinal divisions. From the large number of cells with nuclei lying obliquely, one would infer that oblique division of the cell often took place. I am unable to discover, however, that such is the case; and it seems extremely probable that the divisional plane of the cell does not always coincide with that of the nucleus.

I have found about 25 cells of the serosa with three nuclei. This seems to be a matter of individual variation in the make-up of the membrane, for all but three of the trinucleate cells were in membranes from the brood of a single scorpion, and membranes from some broods appear to have none. I have in one instance found a *group* of trinucleate cells (Fig. 14, *1*, *2*, *3*, *4*). At this spot nuclear multiplication has outstripped cell multiplication. It is nearly always easy to see which of the two original nuclei has divided, for we find two of the nuclei smaller than the third, and nearer to each other than to the latter. In cell *2*, for instance, the pair of nuclei on the left have arisen from a nucleus occupying a position about midway between them. The same statement would doubtless hold true for the two nuclei on the right in cell *3*, and here the odd nucleus is elongated. When the cell is long and the nuclei all lie in the longitudinal axis, as is the case in cell *1*, it is usually impossible to determine which of the two original nuclei has divided; for the nuclei are equidistant, and nearly alike in size. Another type of equidistant nuclei is shown in cell *4*, — a distribution quite as characteristic of very large, broad cells as the linear arrangement is of elongated cells. I have spoken of the division of one of the two original nuclei as though it always took place *after* the nuclei were completely separate, and had taken their positions in the cell. This seems to be the usual method, for I have several times found one of the original nuclei in the act of dividing. But it is possible, of course, for them to arise by a tripartite division, in which the three nuclei would be formed simultaneously. I have found only one instance of a true triple division, represented in Figures 29 and 30, and as this occurred in a serosa which had plainly undergone degeneration, I do not consider it as altogether normal. It will be noticed that the original nucleus became trilobed, and that the lobes became daughter nuclei of approximately equal size by the formation of three divisional planes, meeting at the centre of the original nucleus. The daughter nuclei on the right are still united to each other by strands at the corners. Very similar tripartite divisions were found by Overlach ('85, Plate XI. Figs. 35 and 41) in the epithelium of the cervix uteri. In two other cases, I have found one of the daughter nuclei in a late stage of division (Figs. 31, 32) *itself* elongating and undergoing constriction. It will be noticed that the constricted daughter nucleus is considerably larger than its mate.

I have found but two cells with more than three nuclei, and these both contained four. This condition is brought about by the division of both nuclei of a binucleate cell. On *a priori* grounds, one would reason that quadrinucleate cells would be nearly as abundant as those with three nuclei, for, apparently, it must often happen that a pair of daughter nuclei, arising as they do by a symmetrical and accurate constriction, are ready to divide at almost the same moment. Yet there are doubtless influences which operate to prevent the division of one of the nuclei. Although it is of course impossible to generalize on the characteristics of quadrinucleate cells, it may be of interest to mention the peculiarities of the two found. They are both large cells, of nearly equal width at the ends, and the breadth of both exceeds half the length. In one, both pairs of nuclei lie transversely, showing that the second divisional plane was at right angles to the first. In the other, represented in Figure 33, the lower pair of nuclei lie in the longitudinal axis, the upper pair almost transversely. One of the quadrinucleate cells is considerably larger than any cell near it, while the other (Fig. 33) though by no means small, is of much less dimensions than the immense bi- and uninucleate cells around it. I am unable to assign any reason for the multinuclear condition of this cell. One fact, however, is worthy of note. The united volume of its four nuclei does not exceed the bulk of the *single* nucleus of a neighboring cell. One cannot, of course, ascertain what the size of the primitive nucleus of the multinucleate cell was, but it is very improbable that it exceeded in volume the nucleus of the uninucleate cell in question, for the latter cell is considerably the larger of the two, and throughout this serosa the size of the nuclei bears a direct ratio to the size of the cells.

As regards the influence or influences impelling nuclei to divide independently of the division of the cell, nothing very definite can be stated. It is certain that the *absolute* or *relative size* of *the cell has little or no influence upon the division of the nucleus.* There are cells of all sizes, from the largest to the very smallest (Fig. 3), which are binucleate; and it is usual to find, side by side with bi- or multinucleate cells, others with a single nucleus that are actually larger than the former (compare the cells in Figure 14). In such cases, the single nucleus is always larger than the daughter nucleus of the other cells. I am unable to see that multiplication of nuclei in the cell leads to any immediate increase of nuclear material. The more they divide, the smaller they become. Probably the most important office of division is *a more extensive distribution of nuclei throughout the cytoplasm, with corresponding increase of nuclear surface;* and this, considering the great superficial extent of the cells, and the comparatively small size of the nuclei (at least in the older membranes) must be a matter of some importance for the activities of the cell. It is especially so in the case of *elongated* cells. If such cells have but a single nucleus, a large part of the cytoplasm must be remote from it; and if the nucleus is at the centre of the cell, the cytoplasm at the ends of the cell will be most remote. So, to restore the equilibrium between cytoplasm and nuclei, the nucleus must elongate in the longitudinal axis of the cell, and the daughter nuclei move toward the ends of the cell.

As a matter of fact, nearly all elongated cells have two nuclei, and these lie in the long axis of the cell, usually rather nearer its ends than to each other. It cannot be denied that many short or squarish cells also contain two nuclei; and, conversely, a few much elongated cells can be found that have but one. In the latter case, it is interesting to observe that almost invariably the nucleus has begun to elongate in the longitudinal axis of the cell, and is often far advanced towards division. We can say almost with certainty, then, that such cells are of recent formation, and that the equilibrium between cytoplasm and nucleus is promptly restored by division of the latter. It is true that cases like that represented in Figure 12, where nuclear division takes place in the short axis of an elongated cell, cannot be explained in this manner. Such instances are so rare that they might almost be considered as abnormal; but the difficulty of the matter lies in the fact that we get *all gradations* between nuclei ranged in the true longitudinal axis, and those placed in the transverse axis. It is common to find them lying more or less obliquely in the cell, though the obliquity is seldom so great as to prevent them from practically fulfilling the conditions of the hypothesis.

It is not supposable that all the agencies impelling nuclei to divide, and controlling the direction in which division shall take place, reside in the cytoplasm; possibly the most potent of them exist in the nucleus itself. That axial differentiation, with definite pole and antipole, is as characteristic of the resting nucleus as of the mitotic nucleus, was postulated by Rabl ('85, p. 323) from a careful study of the chromatic network in the "skein stage" of mitosis. In a recent paper ('89, pp. 23, 24), the same writer states that the "polar depression," usually visible in young daughter nuclei, persists much longer than usual in the epithelial nuclei of the Triton; so that for these mitotically dividing nuclei it is highly probable that polar differentiation is *always* present in the resting state. Carnoy ('85) has shown that, in the resting nuclei of the testicular cells of certain Arachnids, the chromatic filaments are distinctly arranged with reference to a definite axis (Planche V. Figs. 165–169), and Van Gehuchten ('89) has found the same in glandular cells of a Dipterous insect, *Ptycoptera contaminata.*

It is obvious that the discovery of an "organic axis," as Van Gehuchten calls it, in amitotically dividing nuclei is more difficult, for here there is no polar depression or longitudinal arrangement of chromatic filaments to indicate its direction in the resting nucleus. It is usual for each division of the nuclei of the serosa to take place at right angles, or nearly so, to the plane of the previous division. This is well seen in many multinuclear cells, where one or both pairs of nuclei lie transversely in the cell, and therefore at right angles, or nearly so, to the direction of the first division (see cells *2* and *3*, Fig. 14). In other cases, however, two consecutive divisions take place in the same direction (Fig. 14, cell *1*). It occurred to me that possibly there was an organic axis in the nuclei of the serosa which in some cases exerted a controlling influence upon the direction in which division took place, but which in most instances was counteracted by influences resident in the cytoplasm. Transverse divisions of the nucleus (Fig. 12) could then be accounted for by assuming that the influence of the organic axis is dominant in these cases, while oblique divisions would be explainable on the ground that neither influence was predominant, but that *both* acted with about equal force in directions at right angles to each other. A question of interest in this connection is, whether, when the cytoplasmic influence is dominant, and tends to make the nucleus divide in a plane parallel to its organic axis, division actually does take place in that direction. If such were the case, an organic axis would be a fact of slight morphological importance, and the longitudinal arrangement of chromatin, which takes place in the earlier stages of constriction (Figs. 4, 6, 7), might occur in any direction, without reference to an organic axis. If, on the contrary, it were necessary that the longitudinal filaments should be arranged *parallel* to the organic axis, in order that division might take place *transversely* to the axis, this result could still be attained by a *rotation of the nucleus*, even when the tendency was for the nucleus to divide at right angles to the previous division. It is obvious that rotation would occasionally be apparent, provided it took place soon after division, and *previous* to the absorption of the proximal end of the connecting filament. I examined a large number of preparations to find evidence of rotation, but I must admit that the evidence was slight, and hardly sufficient to establish the hypothesis which I had formulated. It is therefore put forth provisionally, in the hope that it may lead to further investigations in this line.

The most striking instance of rotation was found in one of the quadrinucleate cells (Fig. 33, nuclei *a* and *b*). It is evident that three nuclear divisions have taken place without any division of the cell, producing two, three, and four nuclei. The arrangement of nuclei makes it reasonably certain that the *lower* pair arose by division of one, and the *upper* pair by division of the other nucleus of the binuclear stage. Only under this supposition could the daughter nuclei of that stage have had the normal arrangement, to which all the neighboring cells rigidly conform. We further find, that, while the upper pair of nuclei has arisen by a division in the long axis of the cell, the lower pair has been produced by division in the transverse axis, and therefore in conformity with the law previously stated (p. 136). One nucleus of each pair (*a* and *b*) retains a remnant of the connecting filament, which is directed, not toward the sister nucleus, but to a point 90° distant from it. This condition could have been brought about only by rotation of the nuclei, which in both cases has been through an arc of 90°.

In the serosæ from older embryos, the daughter nuclei almost invariably recede from each other in the course of division. The amount of recession is governed by the length of the cell (Fig. 15). In the younger membranes, as already stated, the constriction is deep and narrow, so that the nuclei not infrequently lie very near together (Fig. 13). In these young membranes, however, the nuclei are larger, and the cells are usually smaller, than in the old membranes. Since, moreover, the *large* binucleate cells of young membranes almost always have their nuclei symmetrically placed at the ends, it is probable that the nuclei gradually move apart *after* division, as the cell increases in size.

It will be seen that my interpretation of the primary cause of the division of these nuclei agrees in part with the hypothesis advanced by Chun ('90) for the explanation of amitotic division in general. This is, in brief, that the object of amitotic division is the distribution of nuclear material throughout the cytoplasm, with corresponding increase of nuclear surface. He considers it the final phase of a series of conditions which begins with a simple lobed nucleus, and includes branched nuclei of various degrees of complication. In support of this interpretation, Chun lays stress on the statement that cell division, after an amitotic division of the nucleus, has seldom or never been observed with certainty, thereby implying that amitosis cannot have in view the multiplication of cells. I do not consider this as essential to the hypothesis, nor, in fact, do I believe him correct on this point. The evidence of cell division after amitosis seems to me abundant and conclusive. It was observed by F. E. Schulze ('75) in *Amœba polypodia;* by Ranvier ('75), Bütschli ('76), Flemming ('82), Arnold ('87), and others, in leucocytes; by Kükenthal ('85), in the lymphoid cells of Annelids; and by Carnoy ('85), in various cells of Arthropods. As the foregoing shows, there is abundant evidence that, in the serosa of the scorpion, division of the cell *sometimes*, at least, follows amitotic division of the nucleus. Furthermore, the extremely regular and well ordered manner in which the nuclei divide, and the similarity as to size and shape of the daughter nuclei, seem to me decidedly against the notion that the *sole* object of the division is to disseminate nuclear substance in the cytoplasm; for in those cases where amitosis is not followed by division of the cell, and assumably takes place simply for the purpose of dissemination, the nuclear products are very variable as to number, size, and shape.

II. The Amnion.

Plate I. Figs. 1 and 2; Plate II. Figs. 16-20.

The amnion is much thinner than the serosa, and like it is composed of a single layer of flat, polygonal cells (Fig. 1, *am.*). But, while both the cells and nuclei of the serosa have become enormously larger than the blastodermic cells from which they originated, those of the amnion have changed little as regards size. The boundaries of the amniotic cells are not always visible, and I find that preparations, even when hardened and stained in the same manner, show the greatest variation in this respect. As a rule, the cell walls in the amnion are sharply and clearly defined *only* in preparations of membranes from advanced embryos. The same is true of the cell walls of the serosa.

In general, the amniotic cell has but one nucleus, which usually occupies the centre of the cell. Blochmann makes the same statement as to the number of nuclei in each cell, and he found no evidence of division among them. The outline of the nuclei, which measure about 15 μ in diameter, is frequently somewhat irregular or lobed. Like the nuclei of the serosa, they are flattened tangentially (Fig. 2, *nl. am.*); but notwithstanding this, they cause an outward bulging of the cell upon the serosa, as shown in Figure 2. They contain always one or more highly refractive, deeply staining nucleoli. The rest of the scanty chromatic substance is in the form of minute granules, occasionally arranged partly in a very faint network (Fig. 18, *b* and *c*). As in the nuclei of the serosa, chromatic threads frequently unite the nucleoli.

Division of the amniotic nuclei is of rare occurrence. In only one of my preparations are dividing nuclei at all abundant. The division takes place without mitosis, but is of a different type from that of the nuclei of the serosa. The only alteration of the chromatin is possibly a change in the position of the nucleoli; I have not been able to detect any modification of the reticulum. The first sign of approaching division is elongation of the nucleus (Figs. 16 and 18, *a*). A deep narrow constriction appears at the equator of the nucleus (Fig. 17). This is followed by the formation of an equatorial septum, at once partitioning off the nucleus into two daughter nuclei (Fig. 18, *b*). If there are but two nucleoli, it is the rule to find one in each daughter nucleus; but where there are several, they are often unequally apportioned. After the formation of the septum, the daughter nuclei still adhere to each other, and division seems always to be attained by deepening of the equatorial constriction in the plane of the septum (Figs. 18, *b*, *c*, and 19). I have not found any evidence of a recession of the nuclei before division of the cell. Furthermore, the rarity of binucleate cells makes it very probable that cell division follows nuclear division promptly. As in the serosa, division of the cell takes place by the formation of a cell wall without marked constriction (Fig 20). The position of the nuclei in this figure, and the frequency with which nuclei are found near the boundaries of the cells (Fig. 1, *am.*) is evidence of the promptness of cell division after the division of the nucleus.

It is clear that Chun's hypothesis will not hold in this case, for there is even less tendency than in the serosa to accumulate nuclei in the cell. This may be owing in part to the *shape* of the cell, for it is seldom elongated. It would seem that, in case the cell becomes elongated, nuclear division takes place and the cell divides immediately after the nucleus. The orientation of the nuclei with reference to the cytoplasm of their respective cells would then be accomplished by their migration to the centre of the cells.

III. The Ovarian Capsule.

Plate II. Figs. 21-26.

The epithelium of the ovarian capsule is not often easily made out in ordinary stained preparations, for the nuclei of muscle fibres and connective-tissue cells lie not only just external to the epithelial nuclei, but frequently in the same plane with them. In most of my preparations the boundaries of the epithelial cells cannot be seen at all, and I have therefore confined my attention mainly to those which show them distinctly. In shape, the cells are more or less irregular, oblong hexagons (Figures 24 and 25 represent typical shapes). The cell walls are broad and fibrillated, like those of the serosa, though the cells themselves are smaller even than those of the amnion. The nuclei are not only larger in proportion to the cells, but often larger absolutely, than the amniotic nuclei. The amount and arrangement of the chromatin in the capsular nuclei (except in a certain phase) is almost precisely like that already described for the nuclei of the amnion, but there is usually only one conspicuous nucleolus. The small amount of chromatic substance, aside from the nucleolus, has a granular appearance, but sometimes shows indications of a filamentous or reticular arrangement (see Figs. 21, 23, 24). Seen in face view, the nuclei are circular, and have a distinct nuclear membrane. The section (Fig. 2, *nl. fol.*) shows that they are less flattened than the amniotic nuclei.

Here, again, we have amitotic division, and of precisely the same type as prevails in the amnion. Apparently, division is not of common occurrence, for I have been able to find only a few instances, and have, unfortunately, not seen its earliest stages. Figures 21, 22, and 23 show the simple manner in which it is effected. As each daughter nucleus contains a nucleolus, and the ordinary resting nucleus has but one, division of the nucleolus must precede division of the nucleus. In one important respect the division of these nuclei differs from that of the amniotic nuclei. The cell does not divide immediately after the nucleus, and consequently a great number of cells are binucleate. Some even contain three nuclei. I have obtained no evidence whatever of cell division.

IV. Degenerative Changes.

Plate II. Figs. 14, 24–26 ; Plate III. Figs. 28, 34.

The striking difference in the appearance of cells and nuclei, and the different manner of division of the nuclei, exhibited by serosæ of different ages, have frequently been referred to. Such changes, in part at least, I believe to be due to degeneration of the membranes, which, with the exception of the ovarian capsule, are temporary structures, soon to be cast off by the embryo. Hence it is not surprising to find them undergoing degeneration *in toto.* The degenerative changes are about equally well marked in all three membranes; but on account of the great size of cells and nuclei, the changes are most conspicuous in the serosa. If the membrane comes from a young embryo, the walls of the cells are unstainable, and therefore often difficult to make out. The nuclei have a vesicular appearance, with smooth, rounded contour, abundant karyoplasm, and scanty chromatic substance. For this reason the nuclei seldom stand out clearly from the cytoplasm in a stained preparation, often being no darker than the rest of the cell.

Serosæ from somewhat older embryos, while giving no sure signs of degeneration, have nuclei slightly different from those of the youngest membranes. The amount of chromatic substance appears to be larger. It is gathered into denser and more deeply staining masses, and the nucleoli become larger and more stainable (compare Figures 4 and 5, the former from an older membrane than the latter). Many nuclei at this stage become irregular in outline, and are more or less shrunken in appearance, changes which prepare the way for complete degeneration, found in membranes from the oldest embryos. The nucleus here becomes shrunken into a formless mass, which stains deeply and uniformly. This condition seems to be due almost wholly to loss of the karyoplasm, for the nuclear membrane is seen to be drawn closely over the much condensed chromatic substance. The uniformly staining effect, however, is generally believed to be produced by the solution of a part of the chromatin in the karyoplasm ; this is best seen in nuclei that have not completely degenerated, where the deeply stainable solid chromatin is immersed in the less stainable matrix. Not all the nuclei in a membrane are affected to the same degree by the degenerative change. This is shown in Figure 14, where the nuclei of cell *a*, and that of the cell farthest to the left, are more affected than any others. But in the oldest membranes almost every nucleus has undergone extreme degeneration.

It is an interesting fact, that even the most thoroughly degenerated membranes have numerous nuclei in all stages of division. The dividing nuclei have undergone the same degenerative alteration as the rest. It is impossible to state whether these nuclei had begun to divide *after* the regressive change, or had been overtaken by these changes while undergoing division; and it is equally impossible to say whether degeneration would have prevented the nuclei from completing their division. The division is essentially like that of younger nuclei, but often unsymmetrical.

Not all the degenerative changes are confined to the nuclei. The cells also give evidence of modification. Their walls become more distinct, not only because they are denser and thicker, but on account of their stainability with hæmatoxylin. The cytoplasm frequently has a reticulated structure, which is densest about the nucleus. In the oldest membranes, certain large groups of cells have nuclei surrounded by a narrow bright ring, and outside this a much broader halo of a radiating structure, which takes a deeper stain than the rest of the cytoplasm (see Fig. 34). The appearance of the whole is strikingly like that of the "attraction spheres" of ovarian and other cells, but in this case has certainly nothing to do with mitosis. If the cell contains two nuclei, or a dividing nucleus, each daughter nucleus is surrounded by a halo. In early stages of division, however, the elongated nucleus has a single halo. I am unable to account for these appearances; I do not regard them as attraction spheres, but rather as a result of degeneration. The attraction sphere should radiate from a centrosome; here it radiates from the nucleus as a centre. I may state, in passing, that my search for centrosomes in the serosa has been wholly unsuccessful. The pale ring is very generally present around nuclei that have undergone degeneration. It seems to have no intimate connection with the radiating zone, being frequently found where the latter is absent.

The life history of the serosa cells corresponds closely with that of certain cells in the Malpighian vessels of *Aphrophora spumaria* described by Carnoy ('85, p. 219). The cells at the two extremities of the tubes contain nuclei not greatly different from those of young serosæ, but the nuclei of the middle portion are irregular, jagged, and filled with amorphous chromatin. They therefore bear a strong resemblance to the degenerated nuclei of the serosa. Furthermore, the origin of the peculiar nuclei of the middle portion of the Malpighian vessel agrees closely with that of the degenerated nuclei of an old serosa. It is thus described by Carnoy (p. 220): "Sur les petites

larves on rencontre tous les intermédiaires entre les noyaux des extrémités et ceux du milieu. Peu à peu le boyau s'efface, le noyau lui-même se rétrécit et perd la régularité de ses contours à cause du plissement de sa membrane ; à la fin la nucléine ne forme plus à l'intérieur qu'une masse compacte et homogène, à peu près comme cela se présente dans la tête des spermatozoïdes." In both cases the degenerated nuclei are found in stages of division ; in both, the cytoplasmic reticulum is distinct only in old cells, and where these cells are binucleate it is dicentric, with filaments radiating from the nuclei. The *dicentricity* of the binucleate cells is a point to which Carnoy calls special attention (p. 229). He considers that here the radiating filaments of the cytoplasmic reticulum answer to the polar asters of karyokinesis, and that the nucleus has the function of a centrosome. The same reasoning would apply to the degenerated cells of the scorpion's serosa.

The regressive metamorphosis undergone by the epithelial cells of the ovarian capsule (Figs. 24–26) is very peculiar. Here, again, the cell walls are affected in the same way as in the serosa and amnion, for they are not distinctly seen until after the nuclei have degenerated. Nearly all of the epithelial cells of an old capsule have two nuclei, which are dissimilar in size and appearance (Figs. 24 and 25). The smaller takes a rather deep, uniform stain, almost as dark as that of the chromatin of the other. A nucleolus is always present, and frequently minute granules of chromatic substance. The uniformly staining character of the nucleus is doubtless produced by chromatic substance held in solution by the karyoplasm, a condition of common occurrence with degenerating nuclei. The larger nucleus (Figs. 24 and 25) takes only a slight stain, owing to the scantiness of its chromatic substance, which is present in the usual form of isolated granules and an imperfect network. By examination of a large number of cells, I found nuclear differentiation of every degree, beginning with nuclei almost alike in size and stainability (Fig. 24), then passing to examples of marked dissimilarity (Fig. 25), where the pale nucleus has become almost invisible, and the smaller deeply staining one has attained a very sharp, definite outline. As the pale nucleus becomes more and more shadowy, its shape becomes irregular. Near cells of this sort others can be found which contain only a single deeply staining nucleus (Fig. 26), the other having disappeared altogether. In case of trinucleate cells, I have invariably found two of them to be of the pale sort.

I am unable to offer any other explanation of these changes than that they are the result of degeneration or of decreased activity of the tissue.

But why one nucleus should become altered in one way, and the other in an entirely different manner, is difficult to say. A very similar differentiation of nuclei has been observed by Chun ('90) in the egg germs of a Siphonophore (*Stephanophys*). He found only *one* nucleus in the youngest germs, while the middle-sized and larger egg cells contained *two* of different size, the larger being pale, and the smaller staining intensely. The smaller nucleus moves to the periphery of the egg and is no longer visible when the latter is ripe. The larger nucleus persists as the germinative vesicle. In only one instance did he see a stage that showed that the smaller nucleus *budded out* of the larger. Chun compares the small, deeply staining nucleus to the "Stoffwechselkern" (macronucleus), and the pale one to the "Fortpflanzungskern" (micronucleus) of the ciliate Infusoria.

Summary.

1. The embryo of the scorpion is enveloped by three membranes, the ovarian capsule, the serosa, and the amnion.

2. The ovarian capsule is an enlargement of the ovarian tube; the serosa and amnion arise from the blastoderm of the egg.

3. Serosa and amnion are at first distinct, and joined to each other by minute fibres. These afterwards disappear, and the membranes coalesce.

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4. The serosa is composed of immense flat cells, very variable in size and shape. The cell walls are fibrillated.

5. The majority of the serosa cells have two large nuclei of equal size. There are rarely more than two.

6. The nuclei are disk-shaped, have a distinct nuclear membrane, and chromatin in the form of granules and filaments, the latter forming an indistinct reticulum. There are usually several nucleoli.

7. The cytoplasm of the serosa has a distinct reticular structure.

8. Nuclear division in the serosa is amitotic, and takes place by constriction, preceded by elongation of the nucleus. It is followed or accompanied by recession of the daughter nuclei, which remain for some time connected by a fine strand.

9. Constriction of the nucleus is usually accompanied by a longitudinal arrangement of some of the chromatic threads, radiating from the constricted part. The nucleoli are distributed about equally to the daughter nuclei.

10. Nuclear division may be followed by division of the cell, but not often immediately. The cell divides by the formation of a cell wall, either with or without constriction.

11. The binucleate condition of cells is independent of their size; but, in general, the size of the nucleus, or nuclei, is proportional to the size of the cell.

12. Elongated cells of the serosa are generally binucleate. The nuclei almost invariably lie in the long axis of the cell, near the ends.

13. A binucleate cell becomes trinucleate by division of *one* of its nuclei, and quadrinucleate by the division of *both*. Very rarely the division is tripartite, and the three nuclei are produced simultaneously from a single one.

14. Division of the amniotic nuclei is also amitotic, but the constriction is supplemented by a septum at the equator of the elongated nucleus.

15. There is apparently no rearrangement of the chromatic substance. Nucleoli are apportioned equally to the daughter nuclei.

16. Division of the nucleus is quickly followed by division of the cell, so that binucleate cells are not common.

17. The epithelium of the ovarian capsule is composed of small hexagonal or rectangular cells, which frequently contain two or more nuclei.

18. The nuclei are very similar to those of the amnion, but usually contain only one nucleolus.

19. Nuclear division is amitotic, and precisely like that of the amniotic nuclei. Each daughter nucleus contains one nucleolus.

20. No instance of cell division was observed.

21. All three membranes undergo degeneration as the embryos approach maturity.

22. In the serosa the cytoplasmic reticulum becomes more distinct, and is seen to radiate from the nuclei. The cell-walls become stainable.

23. The chromatic substance of the nuclei becomes grouped into dense masses; the reticulum and nucleoli become more distinct. The outlines of the nuclei become irregular.

24. As degeneration proceeds, the cytoplasm frequently forms a halo of radial structure around the nucleus.

25. The nuclei finally become reduced to uniformly staining, irregular masses of chromatin, which has partly entered into solution. Such nuclei are found in all stages of division.

26. In binucleate cells of the ovarian epithelium the nuclei become dimorphic.

27. The chromatic substance of one of the nuclei enters into solution in the karyoplasm, and the nucleus becomes reduced in size.

28. The other nucleus loses its stainability, and increases in size. It finally disappears.

V. Discussion of Amitosis.

As long as karyokinesis was supposed to be a uniform process, all the complicated details of which were carried out with the greatest exactness and in the same sequence, wherever it occurred, no one sought to homologize it with the little known and far simpler "direct" division. The latter had, apparently, so restricted a range, and had received so little attention, that its very existence was denied; and it was generally anticipated that, in the few kinds of cells in which it was stated to occur, a better technique and more careful study would reveal mitotic phenomena. This opinion seemed to receive confirmation by the discovery of mitotic division in leucocytes and the Protozoa, thus carrying mitosis back to the simplest types of cells and to the lowest forms of life. The ascertainment of two facts has brought about a radical change in our views regarding amitosis: (1) the variability of karyokinesis, including, in some cases, the omission of apparently essential steps; and (2) the wide occurrence of amitosis, new instances of which are constantly coming to light in various parts of the Animal Kingdom. Inasmuch as it became necessary to recognize the existence of direct division, efforts were naturally made to find links connecting it with mitosis; the variability of both mitosis and amitosis seemed to lend strength to the theory which refers them to a single fundamental plan of division. In this scheme, amitosis is considered either as a primitive method from which mitosis was evolved, or else is looked upon as a degenerate form of mitosis, occurring in nuclei which, from their pathologic or exhausted condition, have lost the power of dividing by the more complicated process. By fixing epithelium of the salamander larva with osmic acid, then treating it with Müller's fluid, and finally staining with hæmatoxylin, Pfitzner ('86ª) has shown conclusively that, even in cases of very perfect mitosis, the karyoplasm maintains its integrity, and divides by a simple constriction, as in direct nuclear division. This fact has led Waldeyer ('88) to the conclusion that karyokinesis in based upon the simple scheme of division conceived by Remak. He says: "I would interpret the facts in such a way that we have to regard as the fundamental form the simple amitotic division, which is now proved for many cases; it always takes place where the nucleus either is poor in chromatin, or when it does not matter about strict bipartition of the chromatic material. Should the latter be required, then we shall find mitosis, since it is the most direct, most certain, and most simple manner in which an exact bipartition of chromatic substance is brought about."

It seems to me, however, that there are differences of so fundamental a character between mitosis and amitosis, as at present understood, that it is impossible to refer them to a single plan of division. Both, indeed, achieve the same result, — division of the nucleus, including its two constituents, chromatin and karyoplasm. In both cases, the karyoplasm divides by constriction. In amitosis, the chromatin undergoes little if any change in preparation for division; in mitosis it becomes consolidated into a limited number of thickened rods or loops (chromosomes), which arrange themselves in the plane of division ("mother star," "couronne équatoriale") and segment either longitudinally or transversely, the halves moving to opposite poles ("diaster"), and undergoing a reversed metamorphosis to form two daughter nuclei. If this were all there is to karyokinesis, — and in some cases the process is much simpler, — we might hope to find transitions between it and amitosis; for there are examples of amitosis in which the chromatic network undergoes changes during division, and it would be conceivable that the highly organized changes of the chromatic substance during mitosis were either evolved from them, or that they were a simplification of the more detailed changes. In mitosis, however, other structures besides chromosomes make their appearance, — the *centrosomes*, *attraction spheres*, and *spindle*. These structures are not known to take any part whatever in amitosis, and in this respect at least the two kinds of division are fundamentally different. The most recent workers upon karyokinesis agree in assigning to the spindle rays the function of *separating or dividing the chromosomes, and drawing (or pushing) the segments towards the poles.* The centrosomes are focal points towards which the spindle rays converge, and lie *entirely outside the nucleus.* The formation of the spindle has been carefully studied by many investigators of karyokinesis, and, while there are very divergent views as to its origin and mode of action, the most recent workers in this field (of whom

E. van Beneden, Boveri, and Watase may be mentioned) are agreed that the spindle arises *from the cytoplasm.* The same view with regard to the spindle in the mitosis of vegetable cells was expressed by Strasburger, Guignard, and other botanists.

The centrosome, as a converging point for the spindle fibres and polar rays, plays a most important part in karyokinesis, and, so far as known, none at all in amitosis. The centrosome has indeed been found by Flemming ('91) in leucocytes, which certainly divide amitotically; but there it is a single structure, and as Flemming's figures show, *takes no part in the amitotic division of the nucleus.* Whether it also remains passive during the *mitotic* division of leucocytes and in amitosis followed by division of the cell, is not known. It has been supposed by Carnoy ('85) that spindle rays were present in certain nuclei which divide amitotically, but this seems extremely doubtful, especially since they have no perceptible action on the chromatic substance. I believe it can be shown in every case of amitosis known, that the division of the chromatin is accomplished *independently of chromosomes, spindle rays, or any other visible influence outside of the nucleus.*

The persistence of the nuclear membrane in amitosis, and its disappearance in mitosis, were formerly considered points of distinction between the two kinds of division; but, as is well known, more recent studies have shown that the membrane persists in many cases of undoubted karyokinesis, especially among the Arthropods (Carnoy, '85) and Protozoa (Gruber, '83, R. Hertwig, '84, Pfitzner, '86^b, and Schewiakoff, '88). Its presence seems to offer no obstacle to the karyokinetic changes, and Watase ('91) has pointed out that it need not prevent the formation of an extra-nuclear spindle, the rays of which may penetrate the membrane. In the nuclei of *Opalina ranarum*, and in the micronuclei of Infusoria generally, where, according to all observers, the nuclear membrane persists, the mitotic division is accompanied by constriction; but the fact that constriction is here *visible* may be considered as in some measure a *result* of the persistence of the membrane, thereby making evident the outline of the karyoplasm. Yet constriction does not always take place when the membrane persists, for in the spermatic cells of *Pagurus striatus*, figured by Carnoy ('85, Plate VII. Fig. 244), the nuclear membrane is visible at all stages, and gives no evidence of constriction.

The modification of the chromatic substance into chromosomes is usually the most conspicuous feature of karyokinesis, and in most cases serves to distinguish mitotic nuclei from any of the amitotic ones. The chromosomes invariably include *all* the stainable substance of the nucleus, so that the presence of nucleoli in a nucleus undergoing constriction may be taken as perhaps the strongest evidence of direct division. The behavior of nucleoli in amitosis is of peculiar interest. Where there is a single nucleolus, it constricts previous to the constriction of the nucleus, according thus with the Remakian scheme. The division of the nucleolus, however, has rarely been observed. It was first described, I believe, by F. E. Schulze ('75), in the division of *Amœba polypodia;* has since been figured by Carnoy ('85, Plate I. Figs. 10, 12, 13) for various amitotically dividing Arthropod cells, and by Hoyer ('90) for the intestinal epithelium of *Rhabdonema nigrovenosum.* A peculiar modification of the nucleolus, and its division into four segments previous to the constriction of the nucleus, was observed by Platner ('89, pp. 145–149) in the Malpighian vessels of *Dytiscus marginalis.* It is extremely probable that, whenever the nucleolus is a single and definitely organized structure, it always divides previously to or during constriction of the nucleus. Where there are several small nucleoli, they may indeed arrange themselves so as to be equally apportioned to the daughter nuclei; but they are not known to divide, as the chromosomes in mitosis do.

Amitotic division, even more than karyokinesis, is variable in its phenomena. It takes place by constriction, by formation of division planes, by gemmation, and by enlargement of one or more perforations (Arnold, '88, Flemming, '89). It is either simple or multiple, and it may or may not be accompanied by division of the cell. The resulting nuclei may be equal or unequal. Amitosis occurs throughout both the Animal and Vegetable Kingdoms; but as far as animals are concerned, it is far the most frequent among *unicellular organisms, amœboid cells* (*leucocytes*), *and epithelial tissues.* There seem to be no authentic instances of it in connective tissues (except possibly the fat-cells of Arthropods, described by Carnoy), none in nervous tissue, and but one or two in muscle fibres (Carnoy, '85, p. 221). Not only the nuclei of fixed tissues divide by the direct method, but also those of nascent tissues, at least among the Arthropods. Direct division is, however, of rare occurrence in the embryo. I believe there are only two authentic instances of it, — that discovered by Carnoy in the ventral plate of an embryo of *Hydrophilus piceus* ('85, p. 224, Plate I. Fig. 11), and that found by Wheeler ('89, p. 313) in the formation of the blastoderm of *Blatta germanica,* where no instance of mitosis was detected. The embryonal membranes of the scorpion I do not include under this head, because they are temporary structures forming no vital part of the embryo.

Among the Metazoa, epithelial tissues offer by far the greatest number and the most interesting cases of amitosis. Furthermore, as Ziegler ('91) has very recently shown, *epithelial cells of unusual size, with some peculiar functional activity (generally secretion) are most apt to exhibit this method of division.* Cell division has seldom been observed to follow amitosis in such large cells, which therefore become multinucleate. Other epithelial cells which frequently furnish instances of amitosis are those *which are near the end of their functional activity.* Cells of the *outer* layer of a stratified epithelium sometimes divide amitotically, while those of the *deeper* (and therefore *younger*) layers of the same epithelium divide by mitosis. A good instance of this was recently described by Dogiel ('90) in the epithelium of the bladder of Mammals. The nuclei of the large epithelial cells lining the intestine of Arthropods very commonly divide by amitosis, as was found by Frenzel ('85) in the midgut of *Astacus* and *Maja;* by Carnoy ('85) in the intestinal epithelium of Isopods; and by Faussek ('87) in the digestive tract of a Cricket (*Eremobia muricata*) and in the larva of *Æschna.* The intestinal epithelium in all Arthropods has an important secretory function. Cells whose function is excretory likewise exhibit amitotic division of the nucleus, as in the Malpighian vessels of Insects. The occurrence of amitosis in glandular and excretory epithelium is readily explainable on Chun's hypothesis, for the functional activities of such cells are peculiarly intense, and it is easy to see that a distribution of nuclear material in the cytoplasm is of advantage to the cell. The occurrence of nuclei of unusual size (as compared with the nuclei of other cells of the same animal) seems to me likewise referable to the peculiar needs of the cytoplasm in these cells.

Cases of amitosis peculiarly difficult of explanation are those presented by the germinal epithelium of the testis. So many observers have reported direct division in sperm mother-cells, that there seems no reasonable doubt of its occurrence. It has been suggested that the cells which divide amitotically never produce spermatozoa, but merely serve to secrete a fluid. This explanation, however, will not serve in the case of certain Isopods (*Oniscus asellus* and *Idotea* sp.) in the testes of which Carnoy ('85, p. 222) found amitosis the prevailing type of division, and mitosis of very rare occurrence. Direct division is found more or less frequently in the testicular cells of many other Crustacea, as the extensive work of Gilson ('84–87), and the investigations of Sabatier ('85) show, and occasionally in the other groups of the Arthropods. Among Vermes, it was found by Lee ('87) in Nemertians, and by Löwenthal ('89) in a Nematode (*Oxyuris ambigua*). It need hardly be said that amitosis in sexual cells is unexplained by any hypothesis yet offered regarding the biological significance of this type of division, and further investigations on this point are absolutely necessary before we can form any general opinion in regard to it.

In the maturation and segmentation of the ovum no instance of direct division is known, and it is here that karyokinesis is exhibited in its most complete form. The well known observations of Boveri ('87) on the segmentation of the egg of *Ascaris megalocephala* are of special interest on this point. He found a modification of the chromatic threads as early as the two-blastomere stage, one of them (cell A) retaining the four chromosomes characteristic of the nucleus after fertilization, the other (cell B) undergoing a reduction of its chromosomes into the form of granules. The two blastomeres arising by division of cell A undergo the same differentiation, the nucleus of one (cell A^1) retaining the chromatic loops, the other (cell A^2) undergoing reduction, so that in the four-cell stage only one nucleus has retained its chromatic loops. The systematic reduction of chromosomes was observed up to the 64-cell stage. The important deduction Boveri makes from these facts is, that the cells retaining their ancestral nuclear characters are the *Anlage* of the sexual cells of the developing animal, and that the cells whose nuclei undergo a modification of the chromosomes are all somatic cells. In accordance with this hypothesis, the division of both male and female sexual cells ought always to be karyokinetic, and of a somewhat different type from the karyokinesis of the somatic cells of the same animal. The latter statement, indeed, holds true for the testicular cells of the salamander, as was discovered by Flemming ('87). It also appears from the work of Carnoy, that in the post-embryonic life of Arthropods mitotic division is of rare occurrence in the tissue cells, but is of constant occurrence in the reproductive cells of the same forms.

As has already been stated (p. 147), attempts have been made to find a morphological connection between karyokinesis and direct division, and thus to solve the puzzling question of the relations they bear to each other. Carnoy ('85, p. 398) believes he has found transitions between them in the division of the numerous nuclei of *Opalina ranarum.* Some of these show a distinct spindle, others none ; in both cases the nuclear membrane persists, and division is accomplished by constriction. Pfitzner ('86^b), however, found only mitosis in *O. ranarum.* Carnoy has also seen transitional forms of division in the spermatic cells of

Pagurus striatus, and *P. callidus* (Planche VII. Figs. 244, 245). A nuclear plate is here formed, both in perfect mitosis and in degenerated mitosis; but in the former instance a spindle is formed, and the chromosomes segment individually, while in the latter the plate divides *in toto* by constriction, without the help of a spindle. This modified type of mitosis, if we may so regard it, Carnoy considered as the result of degradation (pp. 316, 317), inasmuch as it appeared only in *old* sperm mother-cells after spermatozoa had become numerous in the testis. This accords with the earlier view that direct division is concomitant with senescence of the nuclei, based especially upon nuclear division in plants (Schmitz, '79, Johow, '81). I have regarded this as a possible explanation of the occurrence of amitotic division in the embryonal envelopes of the scorpion, for these tissues are temporary structures which obviously are near the end of their functional activity. This explanation, however, will not fit all cases; for instance, the occurrence of amitosis in embryonic cells, and its prevalence in the testicular cells of some Isopods, already mentioned.

The hypothesis advanced by Chun seems to throw light upon many of the cases of amitotic division which are referable to a sort of *budding* or *branching* of the nucleus, carried to such a point that the buds or branches become constricted off as separate nuclear elements. These cases are, of course, not to be confounded with a disintegration of the nucleus, such as takes place in the macronucleus of Infusoria after conjugation, and sometimes in the degeneration of tissues. The distribution or extension of nuclear substance in the cytoplasm, whereby the surface of the nucleus is increased, is an event of frequent occurrence. It is seen in the many forms of lobed nuclei, such as those of the ovarian capsules of Amphibia (see Flemming, '82), and in those of leucocytes; in hollow or perforated nuclei (giant cells); in branched nuclei (spinning glands and Malpighian vessels of Lepidoptera); and in the band-shaped and moniliform nuclei of many Infusoria. These peculiar shapes are evidently produced by the *activity of the nucleus itself*, probably correlated with a special function of the cytoplasm. From the deeply incised lobation or band-shape of such nuclei it is an easy step to the formation of separate smaller nuclei by the deepening of a constriction already formed. Such daughter nuclei will as a rule be irregular in shape and unequal in size; but if their production subserves a definite and important function, we should expect that in some cases their formation would become a regular process, governed by definite laws. It is possible that the more symmetrical kinds of direct division are to be explained in this way, and such an explanation seems to apply well, as suggested on a preceding page, in the case of the scorpion's serosa. Division of the cell does not follow as a rule, and upon this fact Chun lays stress. But, so far as we know, there is nothing to exclude the *subsequent* occurrence of cell division, and it is even probable that cell division is induced by the presence of more than one nucleus. This I take to be the case in the scorpion's serosa, where I believe the division of the cell is due in part to the dicentricity set up in the cytoplasm by the division of the nucleus.

The study of nuclear division among the Protozoa seems likely to throw much light upon the relations of amitosis to mitosis, for there can be little doubt but that this group presents the most primitive types of nuclear division. So far as known, the very lowest forms of animal cells (*Amœbæ*) always divide by the direct method, as the study of *Amœba polypodia* by F. E. Schulze ('75), and of *Pelomyxa villosa*, *Amœba secunda*, and *A. proteus* by Gruber ('83 and '85), has shown. The division of the nucleus of *Amœba proteus* takes place by a sharp equatorial cleft, passing through the large, centrally placed nucleolus, and dividing that and the peripheral zone of chromatin into two exactly equal halves, which afterwards move apart. This is regarded by Gruber ('83, p. 385) as a simple type of karyokinesis, because an exact division of the chromatin is accomplished. No kinetic change of the chromatic substance is necessary to bring this about, hence none occurs. It seems to me that the absence of centrosomes and a spindle effectually separates this type of division from true karyokinesis, and until these are discovered, the nuclear division of *Amœba proteus* must be relegated to amitosis. The presence of so perfect a type of karyokinesis as that found in *Euglypha alveolata*, worked out so completely by Schewiakoff ('88), is strong evidence against the hypothesis that karyokinesis was gradually evolved from direct division. For here, among the lowest forms of animal life, we have nuclei dividing both by a simple constriction, and by the most highly developed kinetic changes.

Nuclear division among the Infusoria is of special interest, for we regularly find in the same individual nuclei very different in structure and function, — macro- and micronuclei. The former divide directly, the latter by karyokinesis. Apparent exceptions are seen in *Spirochona gemmipara*, where, according to R. Hertwig ('77) the macronucleus divides by karyokinesis; and in *Opalina ranarum*, studied most carefully by Pfitzner ('86^{b}). As only one kind of nucleus is found in Opalina, it is probable, as Bütschli suggests ('88, p. 1500), that these are of the micronuclear type, inasmuch as the division is in all essential respects like that of micronuclei, and in the resting state the nuclei bear no resemblance to macronuclei. The direct division of macronuclei is often accompanied by a longitudinal arrangement of the chromatic filaments, resembling that found in the scorpion's serosa (see Figs. 6, 7, 8). It seems to me that Carnoy is wrong in speaking of these longitudinal filaments as a "spindle," for it has never been shown that they converge to the poles of the nucleus, and frequently they can be resolved into granules, which is never the case with spindle fibres. Their resemblance to the spindle of karyokinesis is deceptive. From their behavior with stains, I regard them as consisting of chromatin, and Bütschli ('88, p. 1526) speaks of this stage of the macronucleus as the "Knäuelstadium," implying that the parallel filaments are chromatic threads.

Among the Vertebrates, amitosis is unusual, and where it exists karyokinesis is generally found to occur in cells of the same kind. It is almost confined to cells *which do not form fixed tissues*, as leucocytes of all kinds, and "giant cells," especially those of the red marrow. It also occurs in testicular cells of Vertebrates. In leucocytes, according to all observers, the nuclear division takes place by constriction, and is frequently accompanied by division of the cytoplasm (Ranvier, '75; Flemming, '82, p. 344; Arnold, '87). But, as the recent work of Flemming ('91) and others shows beyond a doubt, leucocytes also divide by karyokinesis. It is difficult to say whether there is more than a single kind of leucocyte, one dividing directly, the other indirectly, or whether cells of the same kind divide in two different ways. In case of giant cells, it has been shown by Arnold ('84), Denys ('86), Demarbaix ('89), and others, that division occurs both directly and by multiple karyokinesis. Both kinds of division are followed by division of the cytoplasm, leading to the formation of a brood of daughter cells within the mother cell.

After going over the literature of amitosis, taking especial note of the manner of its occurrence and distribution in the Animal Kingdom, I have become convinced that it is not derived from mitosis, and, on the other hand, is not the forerunner of the more complicated process. I consider it another type of division altogether, which, along with karyokinesis, has been transmitted from the simplest forms of life to the most highly organized. While apparently every kind of nucleus may, at some stage of its existence, divide by karyokinesis, many afterwards exchange this type of division for the simpler process. The special conditions which evoke the exchange are very imperfectly understood, and no hypothesis has yet been offered that will explain all the known instances. Some of the hypotheses that have been suggested I have already dwelt upon at length; others, as *scantiness* of chromatin, and even its *entire absence* in the nucleus (Löwit, '90), seem to me still more inadequate.

One fact in favor of the independence of the two types of division is the *sudden change from mitosis to amitosis, without any visible intermediate stages.* Phylogenetically, this is seen in the abrupt transition from the amitotic division of *Amœbæ* to the very perfect karyokinesis of the nearly related *Euglypha.* Ontogenetically, of course, the exchange is far more abrupt. In the conjugation of Infusoria, all divisions of the micronucleus are undoubtedly mitotic, while the *first* (after conjugation) and all subsequent divisions of the macronucleus, *itself formed from modified micronuclei,* are by direct division. Again, the amitosis of the blastodermic nuclei of *Blatta* (Wheeler, '89) is an abrupt change from the perfect mitosis of segmentation. Other instances are the sudden change from mitosis to amitosis in the layers of stratified epithelium, and in the generations of spermatic cells.

Another fact in favor of my view is the *almost universal distribution of amitosis, and its occurrence in many kinds of cells with widely different functions.* It seems more reasonable to suppose that a process so widely extended is *inherited*, and exists potentially in all cells, rather than to look upon it as independently assumed in a multitude of special cases. The latter supposition is opposed to all we know of the transmission of fundamental characters.

While it is evident that both mitosis and amitosis appeared at a very early period of organic life, it is impossible to say which appeared first. But, on *a priori* grounds, we may conclude that the simpler type preceded the more complex.

CAMBRIDGE, September 28, 1891.

It was not until this paper had gone to press that I had access to the recent communications on amitosis by Flemming ('91[a]), Löwit ('91), Verson ('91), Frenzel ('91), and O. vom Rath ('91). In his review of recent work on cell division, Flemming says (p. 139): "Es ist also nicht nur als feststehend anzusehen, dass Amitose vorkommt, sondern auch, dass sie in normal lebenden Geweben vorkommt, und dass sie zur

Zellenvermehrung führen *kann*." When, however, both mitosis and amitosis occur in the same tissue, he considers it probable that only the former is the *normal* method of regeneration and of growth.

The brief papers by Löwit, Verson, and Frenzel are replies to Ziegler's ('91) recent article on amitosis, and contain little that is new. Verson describes briefly the early stages in the spermatogenesis of the silkworm (*Bombyx mori*). He states that the spermatocytes originate from a single large nucleus ("Riesenkern"), which divides repeatedly and unequally by amitosis. The small daughter nuclei thus produced *divide by mitosis*, and at length form the spermatocytes. Frenzel adduces instances of amitosis in the intestinal epithelium of Crustacea and Insects which do not fall within Ziegler's generalizations.

Vom Rath's paper is a valuable contribution to our scanty knowledge of the occurrence of amitosis in spermatogenesis. He shows very conclusively that, in the testis of the crayfish, amitosis does not occur in the generations of sperm-forming cells, but only in abortive nuclei ("Randkerne"), which soon degenerate into an amorphous mass. If such a fate could be established for all amitotically dividing nuclei in the testes of animals, it would be much easier to form a logical estimate of amitosis.

BIBLIOGRAPHY.

Arnold, J.

'84. Ueber Kerntheilung und vielkernige Zellen. Virchow's Arch. f. pathol. Anat., Bd. XCVIII. p. 501.

'87. Ueber Theilungsvorgänge an den Wanderzellen, ihre progressiven und regressiven Metamorphosen. Arch. f. mikr. Anat., Bd. XXX. p. 205.

'88. Weitere Mittheilungen über Kern- und Zelltheilungen in der Milz., etc. Arch. f. mikr. Anat., Bd. XXXI. p. 541.

Blochmann, F.

'85. Ueber directe Kerntheilung in der Embryonal-hülle der Scorpione. Morph. Jahrb., Bd. X. p. 480.

Boveri, T.

'87. Ueber Differenzirung der Zellkerne während der Furchung des Eies von Ascaris megalocephala. Anat. Anz., Jahrg. II. p. 688.

Bütschli, O.

'76. Studien über die ersten Entwickelungs-vorgänge der Eizelle, die Zelltheilung, und die Conjugation der Infusorien. Abhandl. Senckenberg. Naturf. Gesellsch., Bd. X. p. 213.

'88. Protozoa. Abth. III. Infusoria und System der Radiolaria. Bronn's Classen u. Ord. des Thier-Reichs, Bd. I. Abth. 3, p. 1098.

Carnoy, J. B.

'85. La Cytodiérèse chez les Arthropodes. La Cellule, Tom. I. p. 191.

Chun, C.

'90. Ueber die Bedeutung der direkten Kernteilung. Sitzungsber. Physik-ökonom. Gesellsch. Königsberg i. Pr., Jahrg. 31, 6 pp.

Demarbaix, H.

'89. Division et dégénérescence des cellules géantes de la moëlle des os. La Cellule, Tom. V. p. 27.

Denys, J.

'86. La Cytodiérèse des cellules géantes et des petites cellules incolores de la moëlle des os. La Cellule, Tom. II. p. 245.

Dogiel, A. S.

'90. Zur Frage über das Epithel der Harnblase. Arch. f. mikr. Anat., Bd. XXXV. p. 389.

Faussek, V.

'87. Beiträge zur Histologie des Darmkanals der Insekten. Zeitschr. f. wiss. Zool., Bd. XLV. p. 694.

Flemming, W.

'82. Zellsubstanz, Kern- und Zelltheilung. Leipzig, F. C. W. Vogel.

'87. Neue Beiträge zur Kenntniss der Zelle. Arch. f. mikr. Anat., Bd. XXIX. p. 389.

'89. Amitotische Kerntheilung im Blasenepithel des Salamanders. Arch. f. mikr. Anat., Bd. XXXIV. p. 437.

'91. Ueber Theilung und Kernformen bei Leucocyten, und über deren Attractionssphären. Arch. f. mikr. Anat., Bd. XXXVII. p. 249.

'91^{a}. Ueber Zellteilung. Verhandl. Anat. Gesellsch., 5. Versamm., p. 125.

Frenzel, J.

'85. Ueber den Darmkanal der Crustaceen, nebst Bemerkungen zur Epithelregeneration. Arch. f. mikr. Anat., Bd. XXV. p. 137.

'91. Zur Bedeutung der amitotischen (direkten) Kernteilung. Biol. Centralb., Bd. XI. p. 558.

Gehuchten, A. van.

'89. L'Axe organique du noyau. La Cellule, Tom. V. p. 177.

Gilson, G.

'84–'87. Étude comparée de la spermatogénèse chez les Arthropodes. La Cellule, Tom. I. p. 11; Tom. II. p. 83; Tom. IV. p. 1.

Göppert, E.

'91. Kerntheilung durch indirekte Fragmentirung in der lymphatischen Randschicht der Salamandrinenleber. Arch. f. mikr. Anat., Bd. XXXVII. p. 375.

Grüber, A.

'83. Ueber Kerntheilungsvorgänge bei einigen Protozoen. Zeitschr. f. wiss. Zool., Bd. XXXVIII. p. 372.

'85. Studien über Amöben. Zeitschr. f. wiss. Zool., Bd. XLI. p. 186.

Hamann, O.

'90. Monographie der Acanthocephalen. Teil I. Jena. Zeitschr., Bd. XXV. p. 113.

Hertwig, R.

'77. Ueber den Bau und die Entwickelung der Spirochona gemmipara. Jena. Zeitschr., Bd. XI. p. 149

'84. Ueber die Kerntheilung bei Actinosphaerium eichhorni. Jena. Zeitschr., Bd. XVII. p. 490.

Hoyer, H.

'90. Ueber ein für das Studium der direkten Kerntheilung vorzüglich geeignetes Objekt. Anat. Anz., Jahrg. V. p. 26.

Johow, F.

'81. Die Zellkerne von Chara foetida. Bot. Zeit., Jahrg. XXXIX. Nos. 45, 46.

Kowalevsky, A., und M. Schulgin.

'86. Zur Entwicklungsgeschichte des Skorpions (Androctonus ornatus). Biol. Centralb., Bd. VI. p. 525.

Kükenthal, W.

'85. Ueber die lymphoid Zellen der Anneliden. Jena. Zeitschr., Bd. XVIII. p. 319.

Laurie, M.

'90. Embryology of a Scorpion (Euscorpius Italicus). Quart. Jour. Micr. Sci., Vol. XXXI. p. 105.

Lee, A. B.

'87. La Spermatogénèse chez les Némertiens. Recueil zool. Suisse, Tom. IV. p. 409.

Löwenthal, N.

'89. Ueber die Spermatogénèse von Oxyuris ambigua. Internat. Monatsschr. f. Anat. u. Physiol., Bd. VI. p. 364.

Löwit, M.

'90. Ueber Amitose (directe Theilung). Centralb. f. allgem. Pathol. u. pathol. Anat., Bd. I. p. 281.

'91. Ueber amitotische Kernteilung. Biol. Centralb., Bd. XI. p. 513.

Metschnikoff, E.

'71. Embryologie des Skorpions. Zeitschr. f. wiss. Zool., Bd. XXI. p. 204.

Overlach, M.

'85. Die pseudomenstruierende Mucosa uteri nach acuter Phosphorvergiftung. Arch. f. mikr. Anat., Bd. XXV. p. 191.

Pfitzner, W.

86ª. Zur morphologischen Bedeutung des Zellkerns. Morph. Jahrb., Bd. XI. p. 54.

'86ᵇ. Zur Kenntniss des Kerntheilung bei den Protozoen. Morph. Jahrb., Bd. XI. p. 454.

Platner, G.

'89. Beiträge zur Kenntniss der Zelle und ihre Theilungserscheinungen, I.–III. Arch. f. mikr. Anat., Bd. XXXIII. p. 125.

Rabl, C.

'85. Ueber Zelltheilung. Morph. Jahrb., Bd. X. p. 214.

'89. Ueber Zelltheilung. Anat. Anz., Jahrg. IV. p. 21.

Ranvier, L.

'75 Recherches sur les éléments du sang. Travaux Lab. d'Histol., p. 1.

Rath, O. vom.

'91. Ueber die Bedeutung der amitotischen Kerntheilung im Hoden. Zool. Anz., XIV. Jahrg. Nos. 373, 374, 375.

Sabatier, A.

'85. Sur la spermatogénèse des Crustacés décapodes. Compt. Rend., Tom. C. p. 391.

Schewiakoff, W.

'88. Ueber die karyokinetische Kerntheilung der Euglypha alveolata. Morph. Jahrb., Bd. XIII. p. 193.

Schmitz, F.

'79. Beobachtungen über die vielkernigen Zellen der Siphonocladiaceen. Halle.

Schulze, F. E.

'75. Rhizopoden-studien, V. Arch. f. mikr. Anat., Bd. XI. p. 583.

Verson, E.

'91. Zur Beurteilung der amitotischen Kernteilung. Biol. Centralb., Bd. XI. p. 556.

Waldeyer, W.

'88. Ueber Karyokinese und ihre Beziehungen zu den Befruchtungsvorgängen. Arch. f. mikr. Anat., Bd. XXXII. p. 1. [Transl. Quart. Jour. Micr. Sci., Vol. XXX. p. 159.]

Watase, S.

'91. Studies on Cephalopods. I. Cleavage of the Ovum. Jour. Morph., Vol. IV. p. 247.

Wheeler, W. M.

'89. The Embryology of Blatta germanica and Doryphora decemlineata. Jour. Morph., Vol. III. p. 291.

Woodworth, W. M.

'91. On the Structure of Phagocata gracilis, Leidy. Bull. Mus. Comp. Zoöl., Vol. XXI. p. 1.

Ziegler, H. E.

'87. Die Entstehung des Blutes bei Knochenfischembryonen. Arch. f. mikr. Anat., Bd. XXX. p. 596.

'91. Die biologische Bedeutung der amitotischen (direkten) Kernteilung im Tierreich. Biol. Centralb., Bd. XI. p. 372.

EXPLANATION OF FIGURES.

All figures are from drawings made with the aid of an Abbé camera.

PLATE I.

Fig. 1. Five cells of the serosa, two of them covered by the amnion, which is omitted from the rest of the figure for the sake of clearness. *am.*, amnion; *sr.*, serosa. × 150.

Fig. 2. Section through the embryonal membranes and ovarian capsule. The fibrous appearance of the ovarian capsule is due to the presence of muscle fibres and connective tissue. The boundary line between amnion and serosa is visible only in the vicinity of the amniotic nuclei. *e'th. fol.*, epithelium of ovarian capsule (when the plates were engraved I still took this to be the follicular epithelium, hence the error in the abbreviation); *nl. fol.*, nucleus of capsular epithelium; *nl. sr.*, nucleus of serosa; *nl. am.*, nucleus of amnion. × 630.

Figs. 3–15 are all from the *serosa.*

Fig. 3. Very small, binucleate cell. × 130.

Figs. 4–10. Nuclei at different stages of division. *vac.*, vacuole; *x*, new nuclear wall within the old one. × 550.

Fig. 11. Two cells produced by division of a binucleate cell. × 130.

Fig. 12. Cell from the serosa of a young embryo, with dividing nucleus; the axis of elongation corresponds with the *short* axis of the cell. × 130.

Fig. 13. Cell from serosa of a young embryo, with nucleus unequally divided and daughter nuclei eccentric in position. × 130.

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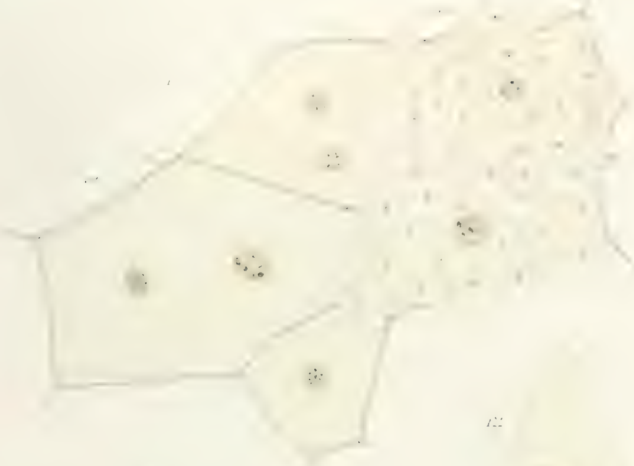

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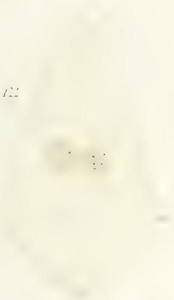

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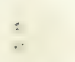

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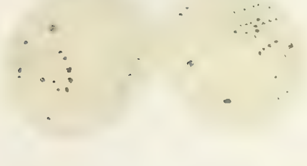

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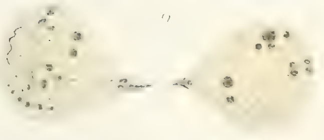

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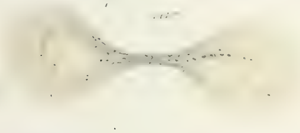

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H.C.J. del.

E. Meisel, lith. Boston

PLATE II.

Fig. 14. Piece of the serosa from an advanced embryo, with four adjacent trinucleate cells (1, 2, 3, 4); nuclei of cell *a* and the large cell farthest to left have undergone degeneration. × 90.

Fig. 15. Three cells of the serosa from an old embryo to show recession of daughter nuclei towards the ends of the cells. × 90.

Figs. 16–20 are from the *amnion.*

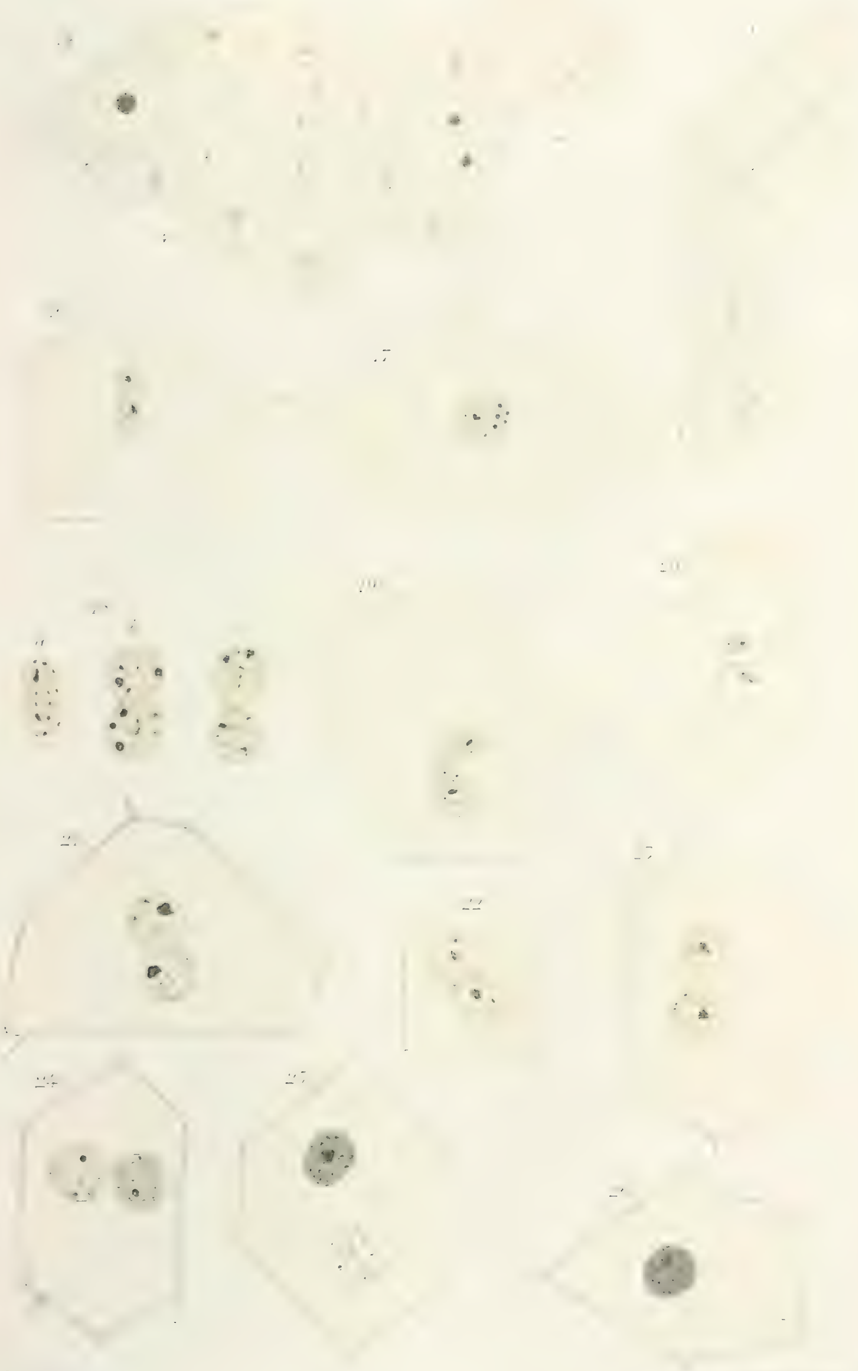
Figs. 16–19. Stages in the division of amniotic nuclei. In Figure 18 three stages are shown, *a*, *b*, *c*. × 800.

Fig. 20. Two amniotic cells, apparently formed by recent division. × 375.

Figs. 21–26 are from the *capsular epithelium.*

Figs. 21–23. Cells showing successive stages of nuclear division. × 800.

Figs. 24–26. Cells to show the degeneration of nuclei. In Figure 24 the nuclei are but slightly differentiated; in Figure 25 the pale nucleus has become much larger and very faint; in Figure 26 it has disappeared altogether. × 800.



H. P. J. del.

E. Meisel lith. Boston

PLATE III.

Figs. 27–34 are all from the *serosa*.

Fig. 27. A cell undergoing division by formation of a cell plate. The daughter nuclei are still united by a connecting thread. The dotted line on the left indicates the edge of the fragment of membrane in which this cell occurs. From the serosa of an advanced embryo. × 304.

Fig. 28. A cell divided by constriction, without the formation of a cell plate. The nuclei have undergone degeneration. From the serosa of an advanced embryo. × 150.

Fig. 29. A cell, the nucleus of which has undergone tripartite division. From an old serosa. × 150.

Fig. 30. Nucleus of the same, more highly magnified. The chromatin is grouped in granular masses. Two of the daughter nuclei are still united by strands of the nuclear membrane. × 630.

Figs. 31–32. Constricted nuclei from a young serosa. One of the daughter nuclei of each is larger than its mate, and has itself become elongated and constricted. × 304.

Fig. 33. Quadrinucleate cell. The upper of the two original nuclei has divided in a longitudinal, the lower in a transverse plane. Nucleus *a* still shows a remnant of the connecting thread, and nucleus *b* retains the conical form it had in division. Both nuclei have rotated 90° from the plane of elongation. × 304.

Fig. 34. Cell from the serosa of a far advanced embryo. The nuclei have undergone extreme degeneration. Each nucleus is surrounded by a bright ring, outside of which is a broad zone of a radiate structure, more stainable than the rest of the cytoplasm. × 150.

No. 4. — *A Fourth Supplement to the Fifth Volume of the Terrestrial Air-Breathing Mollusks of the United States and Adjacent Territories.* By W. G. Binney.[1]

The following pages are believed to contain all that has been added to our knowledge of the subject prior to date.

Students are requested to note that in the Third Supplement, p. 214, the figures of *Arionta Diabloensis* and *Bridgesi* are reversed. On p. 225, Explanation of Plate VII., the references E and F are reversed: on p. 226, Explanation of Plate XI., Figures D and G are reversed.

Burlington, New Jersey, July 1, 1891.

Glandina decussata, Desh.

Plate I. Fig 4.

Under the name of *decussata*, specimens are found in most collections which can hardly be referred to that species. I have figured one of them, and its dentition has already been described and figured in my Third Supplement. The shell is readily recognized by its more cylindrical form. Should it prove distinct from *decussata*, I would suggest for it the specific name of *Singleyana*. I received it from Bexar County, Texas, collected by Mr. Wetherby.

Selenites Vancouverensis, Lea, var. Keepi, Hemphill.

Plate II. Fig. 5.

Shell umbilicated, greatly depressed, thin, smooth, shining, transparent, scarcely marked by the delicate wrinkles; very light horn-color; whorls over four, somewhat flattened above and beneath, and scarcely descending at the aperture; spire flat, not rising above the body whorl; suture well impressed; umbilicus moderately large, exhibiting most of the volutions; aperture transversely subcircular, wider than high; lip simple, thickened, sinuous above, very slightly reflected at the base, ends scarcely approached. Width $\frac{5}{16}$ inch, height $\frac{2}{16}$ inch.

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[1] The Terrestrial Air-Breathing Mollusks of the United States and the Adjacent Territories of North America, described and illustrated by Amos Binney. Edited by A. A. Gould. Boston, Little and Brown, Vols. I., II., 1851; Vol. III., 1857. Vol. IV., by W. G. Binney, New York, B. Westermann, 1859 (from Boston Journ. Nat. Hist.). Vol. V., forming Bull. Mus. Comp. Zoöl., Vol. IV., 1878. Supplement to same, in same, Vol. IX. No. 8, 1883. Second Supplement, in same, Vol. XIII. No. 2, 1886. Third Supplement, in same, Vol. XIX. No. 4, May, 1890.

Hills near Oakland, California. One specimen only.

This rare and interesting little shell I collected some years ago. It is a perfect miniature form, in every respect, of *S. Vancouverensis*. I regard it as an extremely small variety of that so called species. It is about the size of the variety of *S. Duranti*, lately described as *S. cœlatus*, Mazyck, but differs very materially in form, sculptnre, and the general texture of the shell. It differs from var. *Catalinensis* in being more robust, larger, and has a smaller umbilicus. I dedicate this pretty little shell to Prof. Josiah Keep, of Mills College, California, who has done so much through his interesting little book to stimulate the study of West Coast shells.

The above is Mr. Hemphill's description, from "The Nautilus," Vol. IV. p. 42, 1890. My figure is drawn from an authentic specimen.

Selenites Vancouverensis, var. **hybridus**, Hemphill.

Shell broadly umbilicated, depressed, slightly convex above, surface shining, polished, of a dark yellowish green color, lines of growth coarse, rib-like and regular on the spire, finer and more irregular on the body whorl, crossed by fine revolving lines that become fainter on the last whorl, suture well impressed; aperture rounded, broader than high, greatly indented above; lip simple, very little reflected below at its junction with the columella, very sinuous above, its terminations joined by a very thin callus. Height $\frac{3}{8}$ inch, breadth 1 inch.

Astoria, Oregon.

In the strong rib-like sculpturing of the spire, depressed form, and sinuous lip, it resembles *sportellus*. In its greater diameter, dark greenish color, and the absence of the decussating sculpture on the last whorl, it approaches *Vancouverensis*.

All our American *Selenites* commence life with a finely granulated shell. When they have attained about two whorls, the striæ begin to appear, and increase in strength as the shell increases in size.

It is well known that all shell-bearing mollusks construct their shells in obedience to the laws of their constitutional characteristics and the environment, among which I include affinity of matter and mechanical skill, the latter a faculty possessed to a greater or less degree by all animals. Some individuals in a colony of shells display greater mechanical skill than others, or possess stronger imitative powers, and closely follow the lines and styles of their forefathers, strictly attending to the details of sculpturing, not omitting a rib or line. Other individuals of the same colony, not having this imitative faculty so strongly developed, may change or vary the form of the shell by constructing it with more convex whorls, generally resulting in a narrower or more elevated shell; or they may flatten the whorls, resulting in a broader and depressed form. Some modification of the umbilicus generally follows the change in the form of the shell. In both cases the sculpturing may be what we call characteristic of the species, or may be more or less modified by the omission of one, two, or more ribs, or the ribs may be more irregular in shape. A few lines may also be dropped, perhaps some added, or the entire surface may be modified in obedience to the laws of the mechanical skill possessed by the individual, and the affinity of matter secreted by the animal, for the purpose of constructing the shell. An examination of a large number of *Selenites concavus,* and of our West Coast forms, convinces one that the entire group of American *Selenites* is the offspring of a single common type.

The above is Mr. Hemphill's description, from "The Nautilus," Vol. IV. p. 42, 1890.

Selenites Duranti, var. Catalinensis, Hemphill.

Plate II. Fig. 3.

I figure an authentic specimen. See Third Suppl., p. 221.

Selenites Vancouverensis, var. transfuga, Hemphill.

Shell very much depressed, planulate, broadly umbilicated, of a dirty white color; whorls 3½ or 4, flattened above, more rounded beneath, with regular strong rib-like striæ; suture well impressed, becoming deeper and channel-like as it approaches the aperture; aperture hardly oblique, slightly flattened above, with a tendency to a corresponding depression below; lip simple, roundly thickened internally, its terminations approaching, forming in some specimens a short columellar lip, joined by a heavy raised callus in very adult specimens. Height $\frac{3}{16}$ inch, greatest diameter $\frac{9}{16}$, lesser $\frac{7}{16}$ inch.

San Diego, California, to Todos Santos Bay, Lower California.

This is the small flat shell that has been distributed as a variety of *sportella,* and also as a variety of *Voyanus.* I find, however, on comparing it with the typical *Voyanus* collected by me last fall, that it is quite a different shell. The ribs are closer and finer than either *sportellus* or *Voyanus,* the umbilicus is much larger, and it is a very much more depressed shell. I consider it, however, a deserter from the Northern forms, and name it accordingly. It is a much larger and a more globose form than *simplilabris* of Ansey.

The above is Mr. Hemphill's description.

Selenites Vancouverensis, Lea.

The only differences that I can detect between this shell and *Selenites concava,* Say, are these. The umbilicus in the California shells is a little more contracted, the color is a shade darker, the striæ are a little closer, stronger, and more regular, and the body whorl is a little more flattened at the aperture. Height $\frac{5}{8}$ inch, breadth $\frac{7}{8}$ inch.

Sonoma Co. to Santa Cruz Co., California.

The above is Mr. Hemphill's description of what he calls *S. concavus,* var. *occidentalis.*

Selenites Vancouverenis, var. tenuis, Hemphill.

Shell broadly umbilicated, depressed, nearly planulate; of a dirty greenish brown color; whorls 5, flattened above, more rounded beneath, the last expanding laterally as it approaches the aperture, and crowded with fine oblique striæ; suture well impressed; aperture rounded, slightly flattened above; peristome simple, hardly reflected below. Height $\frac{1}{8}$ inch, breadth $\frac{7}{16}$ inch.

Napa Co., California.

The small size, nearly planulate form, and thin, lean body whorl as it emerges from the aperture, will serve to distinguish this shell from the other forms of *concavus* found on the West Coast.

The above is Mr. Hemphill's description. He refers all these varieties to *concavus*, but I use the specific name *Vancouverensis* for all Pacific Region forms.

Limax Hemphilli.

Plate III. Fig. 1.

Length (contracted) 19 mm. Mantle long, 9 mm. End of mantle to end of body 9 mm. Foot wide 2 mm. Median tract of foot gray, lateral tracts brown. Median area of foot rather wider than either lateral area. Mantle free anteriorly as far as respiratory orifice. Body tapering posteriorly, not carinate. Mantle somewhat granulose, not concentrically striate. Color dark brown, obscurely marbled with gray; sides anteriorly grayish and paler.

Limax Hemphilli, W. G Binney, 3d Suppl. T. M. V., p. 205, Plate VIII. Fig. E; Plate I. Fig. 13; Plate II. Fig. 3 (1890).

A species of the Pacific Province, having been found from British Columbia to San Tomas River, Lower California, by Mr. Henry Hemphill, in whose honor it is named.

The general outward appearance of this species resembles that of *campestris*, but every specimen examined by me from numerous localities had a peculiarity in its lingual dentition which seems to me of specific value, — the presence of an inner cutting point to the lateral teeth, very much the same as is found in *agrestis*. The anatomy of this species is specifically distinct from *agrestis* in wanting the trifurcate penis sac of the latter, even did its distribution not preclude its being a form of *agrestis*. I have ventured therefore on giving it a specific name.

The penis sac is large, long, gradually tapering to the apex; the genital bladder is globular, on a short, stout duct.

I figure on the plate a variety from San Tomas River, Lower California, called *pictus* by Mr. Cockerell. Its body is pale, reticulated with gray spots; mantle with black or gray spots. Resembling *L. Berendti*, Strebel, from Guatemala.

For lingual dentition, etc., see Third Supplement.

Zonites Shepardi, Hemphill.

Shell umbilicated, very small, depressed; whorls 3 or 3½, shining, transparent, smooth, somewhat flattened; spire scarcely elevated above the body whorl; aperture oblique, oval; peristome simple, acute, its ends hardly approaching; suture well impressed; umbilicus pervious, and moderately large for so small a shell. Great diameter, 2 mm. Height, 1 mm.

Santa Catalina Island, California.

This little shell belongs to the planulate forms, and somewhat resembles a minute *Z. Whitneyi.*

I dedicate it to Miss Ida Shepard in recognition of her active services among the mollusks of Long Beach, Cal., where she resides.

The above is Mr. Hemphill's description.

Zonites Lawæ.

Shell small, umbilicated, globose, flatter below, shining, light horn-colored, marked with coarse wrinkles of growth; spire rounded; whorls 8, gradually increasing, slightly convex, the last excavated below around the umbilicus; aperture oblique, rounded; peristome simple, acute, thickened with callus within. Greater diameter 9 mm., lesser 7 mm.; height 4 mm.

Zonites placentula, part, W. G. Binney, formerly, Terr. Moll. U. S. V., p. 124, Fig. 44; Plate III. Fig. L (dentition).

Zonites Lawi, W. G. Binney, Suppl. to Vol. V. p. 142; Plate II. Fig. E (also, Ann. N. Y. Ac. Sci., Vol. I., Plate XV. Fig. E, as undetermined).

Mountains of Tennessee (Miss Law); a species of the Cumberland Subregion.

Readily distinguished from *placentula* by its larger size, higher rounded spire, greater number of whorls, and more widely excavated umbilical region.

Jaw as usual in the genus.

Lingual membrane (Vol. V. Plate III. Fig. L, as *placentula*) with 25–1–25 teeth; three laterals and one transition tooth.

Zonites Caroliniensis, Cockerell.

Plate III. Fig. 7.

Among the specimens of *Zonites sculptilis* collected in the mountains of North Carolina are many which differ from the type widely enough to be considered a distinct species. Mr. Cockerell suggests for it the name *Carolinensis*, thus describing it: —

This species differs from *sculptilis* in its fewer whorls, straighter columellar margin, less lunate aperture, fewer radiating striæ, and other points. It is figured as *sculptilis* in Manual of American Land Shells, Fig. 231.

Zonites sculptilis.

Plate III. Fig. 9.

For the sake of comparison with the preceeding species, I have given other figures here of the true *Z. sculptilis.*

Zonites Simpsoni, PILSBRY.

Plate I. Fig. 8,

I give an enlarged figure of an authentic individual of this species. For the description see Third Suppl., p. 218.

Zonites Diegoensis, HEMPHILL.

Plate III. Fig. 2.

Shell minute, umbilicated, thin, light horn-colored, with delicate incremental striæ, globose; whorls 3½, convex; base swollen; suture deep; umbilicus broad; aperture narrow, rounded; peristome thin, acute, its ends approximated, the inner one slightly reflected. Greater diameter 3½ mm., lesser 1½; height 1¾ mm.

Near Julian City, San Diego Co., California. On Cuyamaca Mountain, 4,500 feet elevation.

The above is Hemphill's description. My figure is drawn from an authentic specimen.

Zonites cuspidatus, LEWIS.

Vol. V., Fig. in text; Suppl., Plate II. Fig. C.

Shell imperforate, small, slightly convex above, flattened below; light horn color, shining; whorls 6, gradually increasing in size, with wrinkles of growth, the last not descending at the aperture; peristome thin, acute; aperture rounded, bearing within behind the peristome a white callus, on which is one subcentral and a second basal, erect, recurved tooth-like process, separated by a rounded sinus; base often blackish, showing the white callus prominently. Greater diameter 8 mm., lesser 6; height 4 mm.

Zonites cerinoideus, var. *cuspidatus*, LEWIS, Proc. Phila. Ac. Nat. Sci., 1875, p. 334.
Zonites cuspidatus, W. G. BINNEY, Ann. N. Y. Ac. Nat. Sci., Vol. I. p. 359, Plate XV. Fig. C; Suppl. to Terr. Moll. V., Plate II. Fig. C.

Mountains of Tennessee and North Carolina: a species of the Cumberland Subregion.

The tooth-like processes within the aperture, strongly curved towards each other, form an arched space.

Miss Law thus wrote from Philadelphia, Tenn., of this species: "Unlike *gularis*, it seems to be a rare shell, and I find it only by scraping off the surface of the ground in the vicinity of damp mossy rocks. Its habits are more like *placentula* than *gularis*. I never mistake one for a *gularis*, even before picking it up; the thickened yellow splotch near the lip, and the thinner spot behind, showing the dark animal through it, as well as its more globular form, particularly on the base, make it look very different when alive."

Zonites macilentus, Shuttl.

Plate III. Fig. 3.

The individuals of this group are very often difficult to identify, on account of the blending of their specific characters. The typical *macilentus* is distinguished by a very wide umbilicus and a single revolving lamina starting from near the basal termination of the peristome. The figure of *macilentus* in Volume V. shows a second revolving lamina and a much smaller umbilicus. I give here another figure of what appears to me to be the shell described as *macilentus*. How constant are the characters of the species can be shown only by a large suite of individuals.

Tebennophorus Hemphilli.

Plate III. Fig. 4.

I give a figure of the jaw already described by me.

Patula strigosa, Gould, var. jugalis, Hemphill.

Shell umbilicated, depressed with numerous prominent oblique striæ; spire very moderately elevated or depressed; whorls 5½, somewhat flattened above, but more convex beneath, the last falling in front, with two dark revolving bands, one at the periphery and the other above; the body whorl subcarinated at its beginning, but more rounded as it approaches the aperture; suture well impressed; color ashy white, with occasional horn-colored stains; umbilicus large, pervious, showing the volutions; aperture oblique, ovate, but in very depressed specimens the aperture is at right angles with the axis of the shell; peristome simple, thickened, its terminations approaching and joined by a thick heavy callus, making the peristome in very adult specimens continuous. Height of the largest specimens ½ inch, breadth 1 inch. Height of the smallest specimens $\frac{6}{16}$ inch, breadth $1\frac{1}{16}$ inch.

Patula strigosa, var. *jugalis*, Hemphill, The Nautilus, 1890, p. 134, in Binney's 3d Suppl., p. 215, figure.

Banks of Salmon River, Idaho.

This is another interesting form of the very variable *strigosa*. It inhabits stone piles, and other places where it can find shelter and protection against the fatal rays of the summer's sun, close along the banks of the river. It is interesting on account of its very depressed form and the ovate form of the aperture, the heavy callus joining or "yoking" together the extremities of the peristome.

The above is Hemphill's description.

The figure in the Third Supplement is drawn from an authentic specimen.

Patula strigosa, Gould, var. intersum, Hemphill.

Shell umbilicated, sublenticular, depressed, thin, dark horn-color, more or less stained with darker chestnut. Whorls 5½ or 6, somewhat flattened above, more convex beneath, obtusely carinated at the periphery, and bearing numerous coarse oblique rib-like striæ, and two dark revolving bands; suture well impressed; umbilicus large, pervious; aperture oblique, subangulated; peristome simple, thickened, its terminations joined by a thick callus. Height of the largest specimen ½ inch, breadth ¾ inch. Height of the smallest specimen $\frac{5}{16}$ inch, breadth $\frac{7}{16}$ inch.

Patula strigosa, var. *intersum,* Hemphill, The Nautilus, 1890, p. 135.

Bluffs along the banks of Little Salmon River, Idaho.

This shell inhabits stone piles at the foot of a steep bluff back some distance from the river. It seems to be quite rare, as I found but few specimens during the two or three days of my stay in its vicinity, and many of them were dead. I regard it as one of the most interesting shells found by me during the season, for it combines the depressed angulated or keeled forms of the *Haydeni* side of the series with the sculpturing of *Idahoensis,* two shells representing opposite characters in every respect. It thus becomes the companion of *Wahsatchensis,* a beautiful shell, combining the same characters, but much more developed, and connected with the large elevated forms. Var. *intersum* fills the opposite office, by uniting these characters with the small depressed forms. Taken as a whole, this series of shells, as now completed, seems to me to offer the best guide or key to the study of species that the student can have. Every known external character belonging to the genus Helix is so gradually modified and blended with opposite characters, that, if one had the moulding or making of the many and various intermediate forms, he could scarcely make the series more complete than Nature has done herself.

The above is Hemphill's description.

Patula strigosa, Gould, var. globulosa, Cockerell.

Small, globose, dark above periphery, with two bands, transverse grooved striæ rather well marked. Diameter 11½, alt. 8½ mm. Black Lake Creek, Summit Co. The specimen seems immature, but is remarkable as being the only form I have seen in Colorado that is nearer to *strigosa* than *Cooperi.* It is doubtless allied to var. *Gouldi,* Hemphill. (Cockerell.)

Patula strigosa, var. *globulosa,* Cockerell, The Nautilus, 1890, p. 102.

The above is Cockerell's description.

The above varieties of *Patula strigosa* are transversely ribbed. The following are smooth or striate

Patula strigosa, Gould, var. Buttoni, Hemphill.

Plate I. Figs. 2 and 10.

I figure the typical and the toothed forms. See 3d Suppl., p. 220.

Patula strigosa, Gould, var. albofasciata, Hemphill.

Plate IV. Fig. 9.

Shell globose, elevated or depressed; whorls six, convex, with a broad white band at the periphery, which shows just above the suture on two or three whorls of the spire as it passes towards the summit or apex, separating two variable chestnut-colored zones; the upper one in some specimens is often very dark, in others very light passing into horn-color, and broken into blotches, stains, or irregular lines, which pass up a few whorls of the spire and blend with the horn-colored summit; the lower zone spreads towards the umbilicus in irregular stains, often beautifully clouding the base of the shell, or is often broken into irregular revolving lines, and other varied patterns of coloring; striæ rib-like, quite coarse in some specimens, in others finer and closely set together; aperture circular, ovate, and occasionally pupæform; peristome simple, thickened, subreflected at its junction with the columella, and partially covering the umbilicus, the ends approached and often joined by a callus, the peristome sometimes bearing a tooth-like process; umbilicus deep, moderately large, narrower in elevated and broader in depressed specimens; suture well defined. Greater diameter of the largest specimen 17 mm., height, 12 mm.; greater diameter of the smallest 12 mm., height 7 mm.; with all the intermediate sizes.

Box Elder Co., Utah.

Among leaves, brush, and grass, on limestone rock. Altitude, about 4,600 feet above the sea.

This variety of *strigosa* is so very variable in all its characters I find it quite difficult to draw a description that will cover all the individuals which I include in it. I have given the measurements of the largest and smallest specimens, but there are all the intermediates between those figures.

The above is Mr. Hemphill's description. An authentic individual is figured on the plate.

Patula strigosa, Gould, var. subcarinata, Hemphill.

Among the shells recently collected by Mr. Hemphill at Old Mission, Cœur d'Alene, Idaho, was a marked variety of this species, for which Mr. Hemphill suggests the name *subcarinata*. The specimens vary greatly in elevation of the spire, and in the number and disposition of the revolving bands, often quite wanting, as in the specimen figured in the Third Supplement. All have a very heavy shell, the body whorl of which has an obsolete carina which is well marked at the aperture, modifying the peristome very decidedly. See the figure.

In examining the genitalia I find the base of the duct of the genital bladder greatly swollen along a fifth of the total length of the duct.

Mr. Hemphill (The Nautilus, 1890, p. 133) thus describes it : —

> The shell in general form resembles a large, coarse elevated or depressed *Cooperi*. It has six whorls, well rounded above and beneath, and subcarinated at the periphery. The body whorl has two revolving dark bands, one above and the other below the periphery; sometimes the upper band spreads over the shell to the suture, forming a dark chestnut zone that fades out as it passes toward the apex. The peristome is simple, thickened, its terminations joined by a callus; aperture obliquely subangulate; the suture is well impressed. Height of the largest specimen 1 inch, breadth 1½ inches; height of the smallest specimen ¾ inch, breadth 1 inch.
>
> Rathdrum, Idaho.

An authentic specimen is figured in the Third Supplement.

Patula strigosa, Gould, var. bicolor, Hemphill.

Plate IV. Fig. 7.

This shell is a colored variety of the last. It may be characterized as being of a general dark horn-color mingled with dirty white; there are occasional zones of dark horn-color above and fine dark lines beneath, but no defined bands. In some of the specimens the light color prevails, in others the horn-color spreads over the shell in irregular patches. Height ⅞ inch, breadth 1⅛ inches.

Rathdrum, Idaho. (Hemphill.)

Patula strigosa, var. *bicolor*, Hemphill, The Nautilus, 1890, p. 133.

An authentic specimen is figured.

Patula strigosa, Gould, var. lactea, Hemphill.

Plate IV. Fig. 8.

This is a beautiful clear milk-white shell, with 5½ whorls, subcarinated at the periphery. In the elevated forms the aperture is nearly circular, as broad as high; but in the depressed forms the aperture is broader than high, obliquely subangulate. The lip is simple, thickened, its terminations joined by a heavy callus, — the thickening of the lip and callus is a shade darker than the body of the shell. Height of the largest specimen 1 inch, breadth 1⅛ inches.

Rathdrum, Idaho.

The above varieties represent a colony of the largest specimens of the *strigosa* group that I have collected. They are an important and very interesting addition to the series, and serve to confirm my previous views on the relationship of what I call the *strigosa* group. This colony inhabits open places in the dense pine forests of the mountains, overgrown with deciduous bushes. They hibernate among leaves, brush, and roots of trees, and in protected and secure places, generally on the north slopes of the mountains. (Hemphill.)

Patula strigosa, var. *lactea*, HEMPHILL, The Nautilus, 1890, p. 134.

An authentic specimen is figured.

Patula strigosa, var. Utahensis, HEMPHILL.

For locality, see 2d Supplment, p. 30. This is a rough, coarse, carinated variety, figured in Terr. Moll. V., p. 158, Fig. 66. The peristome is sometimes continuous by a heavy raised callus connecting its terminations. It is sometimes smaller and more elevated. (2d Suppl., p. 33.)

Patula strigosa, GOULD, var. depressa, COCKERELL.

Shell flattish, maximum diameter 21⅓, altitude 12½ mm. Specimens of this variety were sent to me by Miss A. Eastwood, who found them in a cañon near Durango, Colorado. The same variety is figured by Binney, Man. Amer. Land Shells (1885), p. 166, Fig. 153. (Cockerell.)

Patula strigosa, var. *depressa*, COCKERELL, The Nautilus, 1890, p. 102.

Patula strigosa, var. albida, HEMPHILL.

Shell broadly umbilicated, greatly depressed, white, tinged with horn-color; surface covered with fine oblique striæ and fine microscopic revolving lines; whorls 6, convex, the last falling in front; spire very little elevated, apex obtuse, aperture oblique, nearly round; peristome simple, thickened, subreflected at the columella, its terminations approaching, joined by a thin callus. Height ½ inch, greatest diameter 1 inch, lesser ¾ inch.

Near Logan, Utah.

Patula strigosa, var. *albida*, HEMPHILL, The Nautilus, IV. p. 17, June, 1890.

The above is Hemphill's description.

Patula strigosa, var. parma, HEMPHILL.

Shell broadly umbilicated, greatly depressed, of a dark dirty horn-color, surface somewhat rough, covered with coarse irregular striæ, and microscopic revolving lines; whorls 5½ or 6, subcarinated throughout, somewhat flattened above, rounded beneath, and striped with two chestnut-colored bands, one above and the other just at the periphery; spire very little elevated, umbilicus moderately large and deep; aperture ovately round, oblique; peristome simple, subreflected, its terminations approaching and joined by a thin callus. Height ½ inch, breadth 1 inch.

Near Spokane Falls, Washington.

Patula strigosa, var. *parma*, HEMPHILL, The Nautilus, IV. p. 17, June, 1890.

The above is Hemphill's description.

Patula strigosa, var. rugosa, Hemphill.

Shell umbilicated, elevated or globosely depressed, of a dull brown ash-color; surface rough, covered with coarse irregular oblique striæ, and microscopic revolving lines; whorls 5, convex, with or without one or two narrow faint revolving bands. In most of the specimens the bands are obsolete; spire elevated, obtusely conical; suture well impressed; umbilicus large, deep; aperture nearly round; peristome simple, thickened, its terminations approaching and joined by a thin callus. Height of the largest specimen ¾ inch, greatest diameter 1 inch. Height of the smallest specimen ½ inch, greatest diameter ¾ inch.

New Brigham City, Utah.

A large rough robust form, with very convex whorls. Some of the specimens so closely resemble *solitaria*, Say, that one not well acquainted with both forms would be easily deceived, and refer it to that species. In its adolescent state the lip is very thin or easily broken, and on the surface of the adult shells these fractures give it a rough and uneven appearance.

Patula strigosa, var. *rugosa*, Hemphill, The Nautilus, 1890, Vol. IV. p. 16.

The above is Hemphill's description.

Patula strigosa, var. carnea, Hemphill.

Shell umbilicated, greatly depressed, dark horn-color, rather solid, shining, surface somewhat uneven and covered with irregular oblique striæ; whorls 5½, convex, the last faintly subcarinated in the depressed specimens, falling in front, sometimes faintly banded, but most of the specimens are plain and without bands; spire subconical, apex obtuse; suture well impressed, umbilicus large; aperture circular; peristome simple, thickened, its terminations well approached and joined by a callus. Height ⅝ inch, greater diameter ⅞, lesser ¾ inch.

Near Salt Lake, Utah.

Patula strigosa, var. *carnea*, Hemphill, The Nautilus, Vol. IV. p. 15, June, 1890.

The above is Hemphill's description.

Patula strigosa, var. fragilis, Hemphill.

Shell umbilicated, elevated or globosely depressed, translucent, thin, fragile, somewhat shining, of a dark horn-color, surface covered by fine oblique striæ; whorls 5, convex, the last descending in front and striped by two dark chestnut bands, one above and the other below the periphery; suture well impressed; aperture oblique; peristome simple, thickened; umbilicus moderate, deep, partially covered by the reflected peristome at the columella. Height of the largest specimen $\frac{9}{16}$ inch, greatest diameter ⅞ inch, lesser ¾ inch.

Near Franklin, Idaho, among red sandstone.

A very thin and almost transparent variety of the very variable *strigosa*. By its peculiar shade, it is very evident that the animal has drawn largely from the red sandstone for the material to build its shell.

Patula strigosa, var. *fragilis,* HEMPHILL, The Nautilus, Vol. IV. p. 17, June, 1890.

The above is Hemphill's description.

Patula strigosa, var. picta, HEMPHILL.

Shell umbilicated, elevated or globosely depressed, of a dirty white color, stained more or less with chestnut; surface somewhat rough and uneven, covered with moderately coarse oblique striæ, and fine revolving lines; whorls 6, convex, subcarinated, with a broad white band at the periphery, and a dark zone of chestnut on the upper side, extending from the peripheral band to the suture, fading out as it traverses the whorls of the spire; beneath, on the base of the shell, it is striped with numerous bands that sometimes extend into the umbilicus, and also into the aperture; spire elevated; apex obtuse; suture well impressed; umbilicus moderately large and deep, broader in the depressed than in the elevated forms; aperture nearly circular; lip simple, subreflected, its terminations approaching and joined by a thin callus. Height $\frac{7}{8}$ inch, greatest diameter $1\frac{1}{8}$ inches, lesser 1 inch.

Rathdrum, Idaho.

Patula strigosa, var. *picta,* HEMPHILL, The Nautilus, Vol. IV. p. 16, June, 1890.

The above is Hemphill's description.

Patula strigosa, var. hybrida, HEMPHILL.

Shell umbilicated, depressed, white, spire horn-color, surface of the shell covered with fine oblique striæ, and widely separated revolving raised lines; whorls 5, flattened above, rounded beneath, the last falling in front, and striped with two faint chestnut bands; suture well impressed; umbilicus large, showing nearly all the volutions; aperture nearly circular; peristome simple, thickened, its terminations approaching and joined by a thin callus. Height $\frac{3}{8}$ inch, diameter $\frac{3}{4}$ inch, lesser $\frac{5}{8}$ inch.

Near Logan, Utah.

This is an interesting shell, as it is the beginning of the forms of *strigosa* that finally develop the revolving lines into prominent ribs, as seen on the surface of var. *Haydeni,* Gabb.

Patula strigosa, var. *hybrida,* HEMPHILL, The Nautilus, Vol. IV. p. 17, June, 1890.

The above is Hemphill's description.

Mr. Cockerell (The Nautilus, 1890, p. 102) mentions by name only the following Colorado forms:—

P. strigosa Cooperi, form *trifasciata,* Ckll. Mesa Co.

P. strigosa Cooperi, form *confluens,* Ckll. West Mountain Valley, Custer Co.; Garfield Co.; Mesa Co.

P. strigosa Cooperi, form *elevata*, Ckll. Delta Co.

P. strigosa Cooperi, form *major*, nov. Shell with diam. 25 mm. Near head of North Mam Creek, Mesa Co., Sept. 14, 1887.

P. strigosa Cooperi, var. *minor*, Ckll. Near Egeria, Routt Co., abundant. It is quite a distinct local race.

Pristiloma, Ancey.

Animal as in Patula.

Shell small, imperforate, horn-color, shining, many whorled; spire depressed conic; aperture sometimes armed with radiating, rather crowded, palatal lamellæ.

Northern and Arctic North America.

Types: *Zonites Stearnsi* and *Lansingi*, Bland.

Formerly *Pristina*, Ancey, and *Anceyia*, Pilsbry, preoc.

Jaw low, wide, slightly arcuate, ends little attenuated, blunt, with numerous crowded broad ribs, denticulating either margin.

Lingual membrane with tricuspid centrals, bicuspid laterals, aculeate marginals, as in *Zonites*.

Separated from *Microphysa* by the ribbed jaw combined with the lingual membrane of *Zonites*: a very unusual occurrence.

Pristina Lansingi, Bland.

Plate III. Fig. 6.

I give a better figure of this species.

Pristiloma Stearnsi, Bland.

Vol. V., figures in text. Suppl., Plate I. Figs. N (dentition) and O (jaw).

Shell minute, imperforate, globose conic, striate, shining, horn-colored; suture impressed; whorls 7, regularly increasing, the last not descending, very globose, swollen below, excavated closely around the imperforate umbilical region; aperture rounded; peristome simple, acute. Greater diameter 4 mm., lesser 3½; height 2½ mm.

Zonites Stearnsi, Bland, Ann. N. Y. Lyc., XI. 74, Figs. 1, 2 (1875).

Microphysa Stearnsi, W. G. Binney, Terr. Moll. V., figs. in text; Suppl., Plate II. Figs. N (dentition) and O (jaw).

Astoria, Portland, Oregon; Olympia, Washington; Alaska. A species of the Oregonian region.

It is larger, more elevated, and more distinctly striated than *Lansingi*, with wider, more rounded, unarmed aperture.

The jaw is of the same type as described under *P. Lansingi*, with over 19 ribs. (Suppl., Plate II. Fig. O.)

The peculiar lingual membrane also is the same as in that species, with four laterals on each side of the central tooth. (Suppl., Plate I. Fig. N.)

Punctum, Morse.

Animal as in *Patula*.

Shell minute, umbilicated, thin, horn-colored, depressed globose; whorls 4, the last not descending; spire slightly elevated; aperture rounded; peristome thin, acute.

Europe and North America.

Jaw slightly arcuate, ends blunt, not acuminated, composed of numerous subequal, overlapping distinct plates.

Lingual membrane as usual in the *Helicidæ;* bases of attachment subquadrate, reflection small, tricuspid in the centrals, bicuspid in the laterals, marginals irregularly denticulated.

Distinguished by the peculiar free plates of the jaw.

There are two species of *Punctum*, *conspectum* and *pygmæum*.

Helicodiscus fimbriatus, Wetherby, var. salmonaceus, Hemphill.

Plate III. Fig. 8.

I give a figure of this variety from an authentic specimen. See 3d Suppl., p. 189.

Anadenus, Heynemann.

Animal limaciform, subcylindrical, tapering behind; tentacles simple; mantle anterior, concealing an internal shell-plate; no longitudinal furrows above the margin of the foot, and no caudal mucus pore; a distinct locomotive disk; external respiratory and anal orifices on the right posterior margin of the mantle; orifice of combined genital system behind and below the light eye-peduncle. (See Plate I. Fig. 1.)

Internal shell-plate small, oval, flat, with posterior nucleus and concentric striæ. (See Plate.)

Jaw with numerous ribs. See Plate III. Fig. 5.

Lingual membrane with tricuspid centrals, bicuspid laterals, and quadrated marginals. (See same.)

Differs from *Prophysaon* by its posterior respiratory orifice, by the position of the genital orifice, and by its locomotive disk.

Himalaya Mountains; recently found in San Diego County, California, by Mr. Hemphill.

It will be remembered that Fischer considers *Prophysaon* a subgenus of *Anadenus*.

The geographical distribution of *Anadenus* would seem to preclude its being found in California, but to that genus only can I refer the species whose description here follows.

Anadenus Cockerelli, Hemphill.

Plate I. Fig. 1; Plate III. Fig. 5.

Length (contracted) 13½ mm.; mantle, length 4½, breadth 2¾ mm. End of mantle to end of body, 8 mm. Foot, breadth 2 mm. Foot with the locomotive disk, being distinctly differentiated into median and lateral tracts. Respiratory orifice slightly posterior on right side of mantle. Genital orifice below right tentacle. No caudal mucus pore. Locomotive disk about half as wide as either lateral area. Sides of foot wrinkled, but not differentiated from lateral areas, nor specially marked, the wrinkles being a continuation of the transverse grooves of the lateral areas. Mantle tuberculate-rugose, oval in outline, bluntly rounded at either end; not grooved as in *Amalia*. Mantle free in front as far as respiratory orifice. Back rather bluntly keeled its whole length; rugæ rather flattened and obscure, consisting of grooves enclosing mostly hexagonal lozenge-shaped spaces, which are themselves rugose. Color uniform brown-black, without markings, except some dark marbling on the lighter sides. The portion beneath and in front of the mantle is pale, and the head and neck have a gray tinge. Foot brown. Shell internal, thinnish, white, oval in outline. Stomach large, swollen, broad. Liver pale ochrey.

Anadenus Cockerelli, Hemphill, The Nautilus, Vol. IV. No. 1, May, 1890, p. 2.
Anadenulus, Cockerell, Ann. Mag. Nat. Hist., Oct., 1890, p. 279.

Cuyamaca Mountains of San Diego Co., California. Mr. Henry Hemphill.

Jaw low, wide, slightly arcuate, ends blunt, anterior surface with about twenty wide, flat ribs, squarely denticulating either margin. (Plate III. Fig. 5.)

Lingual membrane short and narrow. Teeth 20–1–20, of which eight only on either side are laterals. Centrals tricuspid, laterals bicuspid, marginals quadrate, bluntly bicuspid. (Same Plate.)

Prophysaon Hemphilli.

From Portland, Oregon, Mr. Hemphill brought seventy-seven individuals of a slug which may prove a variety of *P. Hemphilli*. They have the tawny color of *flavum*. The internal shell is so delicate, it is impossible to remove it without breaking it. The penis sac is as in *P. Hemphilli*. The mantle is sometimes smooth, sometimes tuberculate; its fuscous lateral bands are sometimes united by a transverse posterior band. Some of the individuals had the tail constricted preparatory to excision. (See below, under *Phenacarion*.)

Prophysaon Andersoni, J. G. Cooper.

3d Suppl., Plate III. Fig. 1? Plate VII. Fig. C; Plate I. Fig. 3 (dentition); Plate IX. Figs. I, J (enlarged surface).

Shield strongly granular-rugose, the respiratory orifice nearly median on its right margin; tail acute, with small gland; reddish gray, the body somewhat clouded with black, the shield paler, clouded, or more usually with a dark band on each side above the respiratory orifice, converging in an elliptic form; a pale dorsal streak; head uniform pale brown, tentacles darker; foot and often the mantle tinged with olive. Length 2.5 inches (Cooper).

Arion Andersoni, J. G. Cooper, Proc. Phila. Ac. Nat. Sci., Plate III. Fig. F.
Prophysaon Andersoni, J. G. Cooper, Pr. Amer. Phil. Soc., 1879, p. 288.
Prophysaon Andersoni, W. G. Binney, Terr. Moll. V., 3d Suppl., Plate III. Fig. 1? Pl. VII. Fig. C; Plate I. Fig. 3 (dentition); Plate IX. Figs. I, J (surface).

A species of the Pacific Province, Straits of De Fuca to Oakland, California.

The characteristic of this species is the light dorsal band, which is not present in *P. Hemphilli*. It has the broad vagina, stout, short, cylindrical penis sac, and genital bladder of *P. Hemphilli*, as well as the foliated reticulations.

In the many living and alcoholic specimens which I have examined, I have failed to detect any appearance of a caudal mucus pore, which Dr. Cooper is confident of having observed, excepting in eight individuals out of thirty collected by Mr. Hemphill on San Juan Island.

Many individuals examined by me are excided as described under *Phenacarion foliolatus*.

Figure 1 of Plate III. of 3d Suppl. was drawn from a specimen received from Dr. Cooper. It represents the true *Andersoni*, distinguished by a light dorsal band, and by genitalia such as I have described for *P. Hemphilli*. The same form, also received from Dr. Cooper, is drawn by Mr. Cockerell on Plate VII. Fig. C. Mr. Cockerell has shown me that I have confounded with it another species, which he proposes to call *P. fasciatum*. See next species.

Specimens collected by Mr. Hemphill at Old Mission, Cœur d'Alene, Idaho, appear to agree with specimens of this species received from Dr. Cooper. The jaw is low, wide, slightly arcuate, with over 12 broad, stout ribs, denticulating either margin. The lingual membrane is given in Plate II. Fig. 2, of 3d Suppl. The central and lateral teeth are slender and graceful. The latter have, apparently, a second inner cutting point, as is found in *Limax agrestis*. I have so figured it, hoping to draw attention to it, and thus settle the question of its being there. On Plate IX. I have given enlarged views of the surface, drawn by Mr. Arthur F. Gray. (See Explanation of Plate IX. Figs. I and J of 3d Suppl.)

Prophysaon fasciatum, Cockerell.

Length (in alcohol) 19 mm. Mantle black, with indistinct pale subdorsal bands, — an effect due to the excessive development of the three dark bands of the mantle. Body with a blackish dorsal band, commencing broadly behind mantle and tapering to tail, and blackish subdorsal bands. No pale dorsal line. Reticulations on body squarer, smaller, more regular, and more subdivided than in *P. Andersoni*, Cooper. Penis sac tapering, slender. Testicle large. Jaw ribbed. (Cockerell.)

Prophysaon fasciatum, Cockerell, The Nautilus, 1890.
Prophysaon fasciatum, W. G. Binney, 3d Suppl. to Terr. Moll. V., p. 209, Plate VII. Fig. A.

Cœur d'Alene Mountains, Idaho; a species of the Central Region.

This species is described by Mr. Cockerell as distinct from *Andersoni*, with which I have formerly confounded it. (2d Suppl. to Vol. V., p. 42.) It has a dark band on each side of the body, running from the mouth to the foot, and a central dorsal dark band. To this must be referred the descriptions of animal, dentition, jaw, and genitalia formerly published by me as of *Andersoni*.

I am indebted to Mr. Theo. D. A. Cockerell for a figure and description of this species. The former is given on Plate VII. Fig. A, while the latter is given here in the words of Mr. Cockerell, whose name must consequently be associated with it as authority.

The animal extends itself into a long, cylindrical worm-like body with obtuse ends; the mantle is covered with minute tubercles.

Jaw low, arcuate, ends blunt; with numerous (over 15) irregularly developed broad, stout ribs, denticulating either margin.

The lingual membrane has 30–1–30 teeth, with about 12 perfect laterals. Centrals tricuspid; laterals bicuspid; marginals with one long, stout, oblique inner cutting point, and one outer short, blunt, sometimes bifid cutting point. Resembling that of *P. Hemphilli*. Another membrane has 50–1–50 teeth.

Mr. Cockerell describes the penis sac as tapering; in specimens examined by me it is cylindrical, as in *Hemphilli*.

The internal shell is thick, easily extracted without breaking.

Phenacarion, Cockerell.[1]

Animal limaciform, cylindrical, blunt before, tapering behind; tentacles simple; mantle large, anterior, pointed behind, concealing a delicate, thin, subrudimentary calcareous shell-plate, easily fractured; no longitudinal furrows along the margin of the foot; a caudal mucus pore; no distinct locomotive disk; external respiratory and anal orifices on the right anterior margin of the mantle; orifices of the combined generative organs behind and below the right eye-peduncle. (See 3d Suppl., Plate VIII. Fig. A.)

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[1] *Phenax* = an impostor, and *Arion*. Cockerell, The Nautilus, Vol. III. p. 126, March, 1890.

Jaw arcuate, with numerous ribs. (Plate IX. Fig. B of same.)

Lingual membrane with tricuspid centrals, bicuspid laterals, and quadrate denticulated marginals. (Plate IX. Fig. C of same.)

Northwestern parts of North America, in the Oregon Region.

Allied to *Prophysaon*, but distinguished by its more anterior respiratory orifice, its rudimentary shell-plate, and decided caudal pore.

Phenacarion foliolatus, GOULD.

Color a reddish fawn, coarsely and obliquely reticulated with slate-colored lines, forming areolæ, which are indented at the sides, when viewed by a magnifier, so as to resemble leaflets; the mantle is concentrically mottled with slate-color, and the projecting border of the foot is also obliquely lineated. The body is rather depressed, nearly uniform throughout, and somewhat truncated at the tip, exhibiting a conspicuous pit, which was probably occupied by a mucus gland. The mantle is very long, smooth, and has the respiratory orifice very small, situated a little in front of the middle. The eye-peduncles are small and short. Length 85 mm.

Arion foliolatus, GOULD, Moll. U. S. Exp., page 2, Fig. 2, *a*, *b* (1852); BINNEY, Terr. Moll., II. 30, Plate LXVI. Fig. 2 (1851); W. G. BINNEY, Terr. Moll., IV. 6; copied also by TRYON and W. G. BINNEY, L. & Fr. W. Sh., I. 377.

Phenacarion foliolatus, COCKERELL, The Nautilus, 1890, III. 126; W. G. BINNEY, 3d Suppl. to Terr. Moll. V., p. 206, Plate VIII. Fig. A; Fig. B (shell-plate); Plate IX. Fig. B (jaw); Fig. C (dentition); Fig. D (genitalia).

Discovery Harbor, Puget Sound (Pickering); Olympia and Seattle, Washington (Hemphill).

Dr. Gould adds to the above description these words (Vol. II. p. 31): "That this animal belongs to the genus *Arion* there can be little doubt, from the peculiar structure of the tail, as represented in Mr. Drayton's figure, and from the anterior position of the respiratory orifice. It is a well marked species, characterized especially by the leaf-like areolæ by which the surface is marked."

It is with the greatest pleasure that I announce the rediscovery by Mr. Henry Hemphill of this species, which has hitherto escaped all search by recent collectors. It has till now been known to us only by the description and figure of the specimen collected by the Wilkes Exploring Expedition, almost fifty years ago, and given in Vols. II. and III. of Terrestrial Mollusks. A single individual was found in December, 1889, at Olympia, Washington, and sent to me living by Mr. Hemphill. It can thus be described. (See Fig. A of Plate VIII. of 3d Suppl.)

Animal in motion fully extended over 100 millimeters. Color a reddish fawn, darkest on the upper surface of the body, mantle, top of head, and eye-peduncles, gradually shaded off to a dirty white on the edge of the animal, side of foot, back of neck, and lower edge of mantle, and with a similar light line down the centre of back; foot dirty white, without any distinct locomotive disk; edge of foot with numerous perpendicular fuscous lines, alternating broad and narrow; mantle minutely tuberculated, showing the form of the internal aggregated particles of lime, the substitute of a shell-plate, reddish fawn-color, with a central longitudinal interrupted darker band and a circular marginal similar band, broken in front, where it is replaced by small, irregularly disposed dots of same color; these dots occur also in the submarginal band of light color. Body reticulated with darker colored lines, running almost longitudinally, scarcely obliquely, toward the end of the tail, and connected by obliquely transverse lines of similar color, the areas included in the meshes of this network covered with crowded tubercles, as in *Prophysaon Andersoni*, shown in Plate IX. Figs I, J. Tail cut off by the animal. (See below.) Excepting its being of a deeper red, it agrees perfectly with Dr. Gould's description.

Mr. Hemphill writes of it: "I have to record a peculiar habit that is quite remarkable for this class of animals. When I found the specimen, I noticed a constriction about one third of the distance between the end of the tail and the mantle. I placed the specimen in a box with wet moss and leaves, where it remained for twenty-four hours. When I opened the box to examine the specimen, I found I had two specimens instead of one. Upon examination of both, I found my large slug had cut off his own tail at the place where I noticed the constriction, and I was further surprised to find the severed tail piece possessed as much vitality as the other part of the animal. The ends of both parts at the point of separation were drawn in as if they were undergoing a healing process. On account of the vitality of the tail piece, I felt greatly interested to know if a head would be produced from it, and that thus it would become a separate and distinct individual." The animal on reaching me still plainly showed the point of separation from its tail (see Fig. A). The tail piece was in an advanced stage of decomposition. I have noticed the constriction towards the tail in many individuals. The edges of the cut were drawn in like the fingers of a glove, after the excision.

The tail of the *foliolatus* having been cut off, I was unable to verify the presence of a caudal pore from this individual. It was plainly visible in another specimen from Seattle.

In the large Olympia individual, the irregularly disposed particles of lime in the mantle, of unequal size, seemed attached to a transparent membranous plate. With care I removed this entire, and figure it. It is suboctagonal in shape (Plate VIII. Fig. B). Under the microscope it appears that the particles of lime do not cover the whole plate; at many points they are widely separated. This aggregation of separate particles is the distinctive character of the subgenus *Prolepis*, to which *foliolatus* would belong if retained in *Arion*.

The genitalia of the large individual from Olympia is figured on Plate IX. Fig. D. The ovary is tongue-shaped, white, very long and narrow; the oviduct is greatly convoluted; the testicle is black in several groups of cœca; the vagina is very broad, square at the top with the terminus of the oviduct, and the duct of the genital bladder entering it side by side; the genital bladder is small, oval, on a short narrow duct; the penis sac is of a shining white color, apparently without retractor muscle; it is short, very stout, blunt at the upper end where the extremely long vas deferens enters, and gradually narrowing to the lower end. There are no accessory organs. The external orifice of the generative organs is behind the right tentacle. (See 3d Suppl., Plate IX. Fig. D.)

The jaw is very low, wide, slightly arcuate, with ends attenuated and both surfaces closely covered with stout, broad separated ribs, whose ends squarely denticulate either margin. There are about 20 of these ribs. (See Plate IX. Fig. B.)

The lingual membrane is long and narrow, composed of numerous longitudinal rows of about 50–1–50 teeth, of which about 16 on each side (Plate IX. Fig. C) may be called laterals. Centrals tricuspid, laterals bicuspid, marginals with one long inner stout cutting point, and one outer short side cutting point. The figure shows a central tooth with its adjacent first lateral, and four extreme marginals.

Phenacarion Hemphilli.

This form is figured on Plate VIII. Fig. C of 3d Suppl. When extended fully, it is 70 mm. long. It is more slender and more pointed at the tail than *foliolatus*. The body is a bright yellow, with bluish black reticulations. The edge of the foot and the foot itself are almost black; shield irregularly mottled with fuscous; the body also is irregularly mottled with fuscous, and has one broad fuscous band down the centre of the back, spreading as it joins the mantle, with a narrower band on each side of the body. The other characters, external and internal, are given below. It loses its color on being placed in spirits, becoming a uniform dull slate-color. Mantle lengthened oval. Shell-plate represented by a group of calcareous grains concealed in the mantle; it is impossible to remove it as one shell-plate. A decided caudal pore.

Phenacarion foliolatus, var. *Hemphilli*, W. G. Binney, 3d Suppl. to Terr. Moll. V., p. 208; Plate VIII. Fig. C; Plate X. Fig. H (genitalia).

Gray's Harbor and Chehalis, Washington, and Portland, Oregon (Hemphill); a species of the Oregon Region.

On the only living one of the lot from Gray's Harbor, the pore was distinctly visible, and is figured on Plate VIII. Fig. C. Usually it seemed more "a conspicuous pit" than a longitudinal slit, as in *Zonites*. At one time I distinctly saw a bubble of mucus exuding from it. It opened and shut, and is still plainly visible on the same individual, which I have preserved in alcohol and added to the Binney Collection of American Land Shells in the National Museum at Washington.

Jaw low, wide, arcuate, ends attenuated, anterior surface with 16 ribs, denticulating either margin.

Lingual membrane as in *foliolatus;* teeth 50–1–50, with 19 laterals on each side.

Genitalia (3d Suppl., Plate X. Fig. H) ; the form from Gray's Harbor has its generative system very much the same as described for *foliolatus* above. The ovary is much shorter and tipped with brown, and is less tongue-shaped. The penis sac tapers to its upper end. The vagina is not squarely truncated above. The system much more nearly resembles that of *Prophysaon Andersoni* (see Terr. Moll., V.) than that of the Olympia *foliolatus.*

Binneya notabilis, J. G. Cooper.

Plate I. Fig. 9.

A new figure is here given, drawn by Mr. Cockerell.

Triodopsis Mullani, Bland, var. Blandi, Hemphill.

Plate II. Fig. 6.

Shell with the umbilicus partially closed, orbicularly depressed; dark horn-color, obliquely striated; spire short, very slightly elevated, nearly planiform; aperture semilunar, at a right angle with axis of the shell, with a very short nipple-like parietal tooth; peristome thickened, white, plain, without teeth and roundly reflected. Height ¼ inch, breadth ½ inch.

Post Falls, and banks of Salmon River, Idaho.

Helix Mullani in form and size resembles very much the common *tridentata* of the Eastern States. Among the various forms it assumes, none are more marked than the little depressed shell before me. It can be very readily separated from the typical *Helix Mullani*, or its other varieties, by its very depressed form, small size, and the absence of the teeth-like processes on the inner margin of the peristome.

I cannot detect any microscopical revolving lines, or tubercles bearing hairs, mentioned by Bland in his description of *H. Mullani.*

The above desciption is by Mr. Hemphill, who furnished me with the specimen figured.

Polygyra septemvolva, var. Floridana, Hemphill.

Shell deeply umbilicated, elevated, globose conic, light horn-color, with numerous fine ribs above, but smooth beneath; whorls 5½ or 6, the last subangular at the periphery; suture well impressed; spire greatly elevated with an obtuse apex;

aperture lunate, well rounded, and nearly circular; peristome reflected, rounded in front, the margins joined by a triangular tooth on the parietal wall. Greater diameter 6 mm., altitude 5 mm.

Oyster Bay, Florida.

This is a small, very elevated form of the *P. cereolus* group.

The above is Mr. Hemphill's description.

Mesodon ptychophorus, A. D. Brown, var. castaneus, Hemphill.

Shell umbilicated, globosely depressed, of a dark chestnut color; surface covered with coarse, irregular, widely separated lines of growth, and crowded, microscopical revolving lines; whorls 5½, convex, the last slightly descending in front, spire elevated; suture well impressed, aperture subcircular; lip white, reflected and partially covering the umbilicus, its terminations approaching; umbilicus small and deep. Height ⅝ inch, diameter 1 inch.

Old Mission and Rathdrum, Idaho.

I regard *H. ptychophorus* as the progenitor of what I call the *Townsendiana* group of West Coast land shells, and this colored variety seems to still further indicate its relationship to *Townsendiana*, for the spire whorls of nearly all the specimens of *Townsendiana* that I have collected are chestnut-colored. *Townsendiana* does not begin to put on its wrinkles until it has made about four revolutions of the shell. The wrinkles are probably due to its environment.

The above is Hemphill's description, from The Nautilus, Vol. IV. p. 41, 1890.

Aglaja fidelis, var. flavus, Hemphill.

Shell umbilicated, elevated, very faintly subcarinated, of a uniform light yellow color throughout, without bands or other stains of coloring; whorls 6½, convex, with coarse oblique striæ, and microscopic irregular revolving lines; peristome reflected below, simple above; aperture roundly ovate; umbilicus moderate, and partially covered by the reflected peristome; suture distinct. Greater diameter 34 mm., altitude 23 mm.

Chehalis and San Juan Islands, Washington; Port Orford, Oregon.

This is a rare and beautiful variety of this well known West Coast land snail.

The above is Mr. Hemphill's description.

Aglaja fidelis, var. subcarinata, Hemphill.

Shell orbicularly depressed; umbilicated; of a deep dark chestnut-color without bands; whorls 6½, convex or somewhat flattened, the last subcarinated at the periphery; striæ coarse, oblique, crossed by numerous well defined wavy revolving lines; peristome simple, thickened above, reflected below, and nearly covering the umbilicus; umbilicus moderate; aperture roundly ovate; suture well impressed. Greater diameter 37 mm., altitude 20 mm.

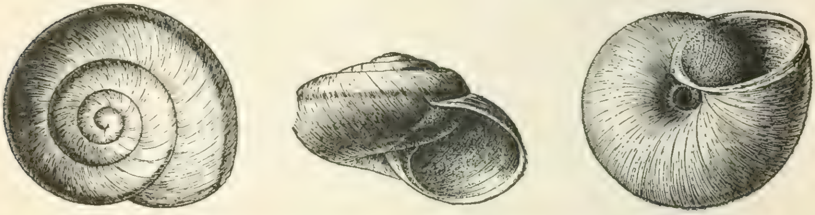
Humboldt Co., California.

This is a very dark, intermediate form of *fidelis*, which in its southern march under changed conditions assumes a more carinated form, and is known to conchologists as *infumata*, Gould.

The above is Mr. Hemphill's description.

Arionta Coloradoensis, Stearns.

Shell orbicular, moderately depressed, whorls slightly elevated, apex obtuse, number of whorls four to four and a half, rounded. Umbilicus narrow, showing the penultimate whorl, though partially covered by the reflection of the lip at the point of junction with the base of the shell. Aperture obliquely ovate, nearly circular, and almost as broad as high. Lip slightly thickened and reflected, or simple, varying in this respect; more reflected and aperture more effuse at the columella.



Parietal wall in the heavier examples calloused, the callus connecting with the inner edges of the outer lip above and below. Shell rather fragile, thin, translucent; surface smooth and shiny, and sculptured with fine incremental lines. Color pale horn to white, and otherwise marked by a single narrow revolving reddish brown band just above the periphery, which in some specimens is obscure or absent. In some individuals certain faint scars upon the upper whorls imply an occasionally hirsute character.

	mm.
Maximum diameter of largest	15.25
Minimum diameter of largest	13.25
Altitude of largest	10.25
Maximum diameter of smallest adult	13.75
Minimum diameter of smallest adult	12.00
Altitude of smallest adult	8.75

Grand Cañon of the Colorado, opposite the Kaibab plateau, at an elevation of 3,500 feet. (Mus. No. 104,100.)

The above, while exhibiting a facies or aspect of its own, its nevertheless suggestive of *H. Remondi*, Gabb, Mazatlan, in the Mexican State of Sinaloa, and also from the high mesas or table lands in the neighborhood of Mulege, Lower California. *H. Carpenteri*, Newcomb, which is a synonym of *H. Remondi*, is credited by the author to "Tulare Valley," and has been found in other localities in California. A glance at the map will show how widely separated geographically *H. Coloradoensis* is from its nearest allies, and this discovery of Dr. Merriam's extends the distribution of the West Coast type of *Helices* farther to the eastward than heretofore, and adds an area of great extent to that previously known.

The above description and figure were published by Stearns in Proc. U. S. Nat. Mus., Vol. XIII. p. 206, Plate XV. Fig. 6, 7, 8, 1890, all copied above.

I have examined the jaw and lingual dentition to find them similar to those of the other species of *Arionta.*

Arionta Traski, var. proles, HEMPHILL.

Shell umbilicated, very much depressed, thin, shining, of a dark horn-color; whorls 5½, somewhat flattened above, convex beneath, the last slightly falling in front, with a dark band above the periphery, and crowded with strong oblique striæ; suture well impressed; umbilicus moderately large and deep; aperture hardly oblique; peristome simple, thin, subreflected, its terminations approaching. Height ⅜ inch, breadth ⅞ inch.

Tulare Co., California, near Fraser's Mill.

A much flatter and more depressed form than any of the varieties of *Traski* that I have seen. There are no revolving microscopical lines, as in *Traski.*

The above is Mr. Hemphill's description.

Arionta tudiculata, var. Tularensis, HEMPHILL.

Shell umbilicated, very thin and frail, shining, of a light greenish horn-color, globosely depressed; whorls 5½, convex, the surface minutely granulated, and crowded with fine oblique striæ, with a single chestnut revolving band; suture well impressed; umbilicus very small; aperture oblique, subcircular; peristome simple, hardly thickened, its columellar portion expanding and nearly covering the small umbilicus. Height ⅝ inch, breadth ⅞ inch.

Tulare Co., California.

This is one of those puzzling intermediate forms uniting two species that can be with equal propriety placed in one or the other. It has the exact form of the typical *Traski* found at Los Angeles, and along the coast, though much smaller and thinner, and it has the sculpturing of *tudiculata* much modified. It seems to fill the gap quite completely between those two species.

The above is Mr. Hemphill's description.

Arionta tudiculata, BINNEY.

Plate II. Fig. 7, 8.

New figures are here given of the form *cypreophila.*

In The Nautilus, Vol. IV. p. 41, 1890, Mr. Hemphill also describes a var. *subdolus* thus: —

Shell narrowly umbilicated; globosely depressed, of a dark yellowish color, surface somewhat shining, covered with oblique striæ, interrupted by numerous wavy lines and oblong blister-like wrinkles, hardly perceptible to the naked eye; whorls $5\frac{1}{2}$, convex, striped by a single chestnut band, double margined by lighter ones; spire very little elevated, suture well impressed; lip simple, reflected, and nearly covering the umbilicus, its terminations approaching and joined by a thin callus; umbilicus narrow and small. Height $\frac{5}{8}$ inch, greatest diameter 1 inch, lesser $\frac{7}{8}$ inch.

San Jacinto Valley, San Diego Co., California.

A very depressed form, quite variable in size, some of the specimens not being more than half the size of the measurements given. It is lighter colored than any of the southern varieties of *tudiculata* except var. *Binneyi.*

Arionta Ayresiana, NEWCOMB.

Plate I. Fig. 7.

I give a new figure of this species.

Arionta intercisa, W. G. BINNEY.

In "Zoe," Vol. I. No. 11, January, 1891, p. 330, Mr. Hemphill describes these varieties of *A. intercisa*: —

Var. *minor.* Smallest specimen, greatest diameter 18 mm., altitude 11 mm. Uniform light yellowish chestnut-color, with and without a band, and varies very much in form and elevation or depression of spire.

Var. *elegans.* Uniform ashy buff-color, faintly banded, and variable in form.

Var. *nepos.* Uniform ashy white; spire horn-color, variable in form and sculpturing.

Var. *albida.* Uniform milk-white, sometimes with a faint band at the periphery; sculpture nearly obsolete.

In the same journal (p. 434) Mr. Hemphill thus describes several varieties of *redimita,* which species he refers, however, to *Kelletti*: —

Var. *castaneus.* Uniform, polished, chestnut-color, darker band at the periphery, spire sprinkled with fine ashen specks.

Var. *hybrida.* Uniform ash-white color, and a dark band at the periphery, flecked with transverse markings and specks of dark brown and light chestnut.

Arionta ruficincta, GABB.

Plate I. Fig. 3.

A new figure is given of this species.

Arionta Kelletti, FORBES.

Mr. Hemphill, in Terr. Moll. V., 3d Suppl., has thus described several varieties. I figure authentic specimens of each.

Var. *albida* (Plate IV. Fig. 3). This is a beautiful clear white translucent variety, with no markings or stains of any kind. It is quite thin and frail, and a trifle smaller than the average size of *Kelletti.*

Santa Catalina Island, California. Two specimens only found by me.

Var. *castanea* (Plate IV. Fig. 4). Among the numerous patterns of coloring assumed by *H. Kelletti,* none are more conspicuous than this well marked variety. The body whorl is of a deep shiny chestnut-color above the periphery, and becomes lighter as it follows the whorls of the spire to the apex. The band at the periphery is quite variable in the different specimens; it is generally light and well defined above, but below it is irregular, and spreads over the base of the shell more or less.

Santa Catalina Island, California. This variety is not rare.

In "Zoe," Vol. I. No. 11, pp. 333, 334, Mr. Hemphill has also thus described several other forms.

Var. *nitida* (Plate IV. Fig. 2). Uniform, translucent, shining, dark horn-color, with a poorly defined dark band, coalescing with a poorly defined whitish band below it, at the periphery; spire faintly flecked with ashen gray.

Catalina Island.

Var. *multilineata* (Plate IV. Fig. 1). Shell marked by alternate shades of ashen white, chestnut, or brown, arranged in an irregular series of revolving and sometimes wavy lines, with a broader and poorly defined band at the periphery; markings finer beneath than above.

Var. *frater.* Shell of a beautiful, uniform, horn-buff color, sometimes fading into lighter horn-color, with a darker band at the periphery, and numerous faint, alternate revolving lines of ashen or dark horn-color above and below; generally, not always, lighter colored beneath, and sometimes with a whitish zone beneath the band at the periphery.

Var. *Californica.* The shell is colored with a darker shade of uniform buff than the above, dark band at the periphery, generally uniform in color above and below; sometimes flecked with squarish dots.

Var. *Forbesi.* Ground coloring whitish buff, with a revolving series of poorly defined and coalescing lines, bands, and blotches.

Var. *bicolor.* Color very dark horn or brownish, flecked with numerous revolving very fine dots or irregular lines, with or without a very faint band at the periphery.

Var. *tricolor.* Irregularly painted with numerous revolving whitish, brownish, and chestnut flecks, blotches, and stains, with or without a band at the periphery.

Var. *albida.* (See below.)

Var. *albida, a.* Milk white ground, very faintly stained with light horn, and with poorly defined and fading lines.

Mr. Hemphill considers *redimita* as a form of *Kelletti.* (See that species.)

Euparypha Tryoni, Newc.

Mr. Hemphill has thus described several varieties. (See Zoe, Vol. I. pp. 331, 332.)

Var. *varius*. The upper or dark zone is of a lighter shade of bluish brown or chestnut than the type, and is flecked and sprinkled with ashen white; band at the periphery dirty white beneath.

Var. *nebulosa* (Plate IV. Fig. 5). Lighter colored above than var. *varius*, marbled and clouded with various patterns of dark brown and dirty white; dirty white beneath.

Var. *fasciata* (Plate IV. Fig. 6). Uniform light chocolate above and beneath, with a dark band at the periphery.

Var. *Californica*. Creamy buff-color, darker above than below the periphery, very faintly banded.

Var. *albida*. Uniform creamy, and sometimes milk-white above and beneath, and without band.

Var. *subcarinata*. Among the subfossils that occur on Santa Barbara Island we find a form of *H. Tryoni* which adds an interesting link to its history and to its present form. It may be characterized as follows. Shell depressed globose, consisting of about $5\frac{1}{2}$ whorls, the last subcarinated at the periphery; in other respects closely resembling the recent form. Greater diameter 23.15 and 20.11 mm., largest and smallest specimens.

Pomatia Humboldtiana, Val.

Texas, at Altuda, at an elevation of 5,000 feet, where it, a single specimen in fair condition, had been thrown out with soil by a prairie dog. (Mus., No. 118,366.) William Lloyd.

This species has not before been reported from any locality within the territory of the United States. It was described from Mexico, where it is found in the neighborhood of the city of Mexico, and in other localities. The national collection contains several examples from the Real del Monte. It has a pretty close resemblance to some of the varieties of the European *H.* (*Pomatia*) *pomatia*, and it may possibly be an introduced form. *H. pomatia* has for centuries been esteemed as an article of food in various parts of Europe, and was regarded as a dainty by the ancient Romans. It was propagated and raised in large quantities for their use, and specially fed on certain plants to give the flesh a particular flavor.

Unmistakable specimens of another favorite edible snail common to Europe, *H.* (*Pomatia*) *aspersa*, is found in Mexico, and examples from Puebla, in the province of Puebla, Mexico, were presented to the National Museum by the Mexican Geographical Commission a few years ago. The presence of these two forms most certainly suggests the question as to whether they were not introduced by the Spaniards many years, centuries, ago, either for food purposes or incidentally in the routine and accidents of commercial intercourse.

The above was published by Stearns in Proc. U. S. National Museum, Vol. XIV. p. 96, 1891. It will be remembered that *Helix Buffoniana* was figured as *aspersa* by Dr. Binney in Volume III.

Bulimulus Ragsdalei, Pilsbry.

Plate II. Fig. 9.

It is about the size and form of *B. Mooreanus*, but rather more slender and elevated. The surface is not smooth, as in the other American *Bulimuli*, but strongly ribbed-striate longitudinally. The apex is blunt; peristome thickened within; columella reflexed over the narrow but open umbilicus. The aperture is less than half the length of the shell; color brownish, corneus somewhat translucent, the riblets opaque white. Height 22 mm., diam. 10 mm.; height of aperture 10½ mm., diameter 7 mm.

Bulimulus Ragsdalei, Pilsbry, The Nautilus, Vol. III. p. 122, March, 1890. Proc. Acad. Nat. Sci. Phila., 1890, p. 296, Plate V. Fig. 3.

St. Jo, and at Warren's Bend, twenty-five miles from Gainesville, and in Cook and Montague Counties, Texas (Ragsdale).

A figure of an authentic specimen is given 1½ the natural size. The description is a copy of the original.

Bulimulis Dormani.

Plate I. Fig. 6.

A new figure is given.

Rhodea Californica.

This extralimital species has actually been received by Dr. Cooper from Lower California. (Proc. Cal. Acad. Nat. Sci., 1891, p. 102.) It had been quoted as an Achatina from Monterey. (See Vol. V.)

Pupa Californica.

Dr. Sterki in Nautilus, Vol. IV. page 7, mentions a variety, *elongata*, from San Clemente Island; on page 18, varieties *trinotata*, *Diegoensis*, and *cyclops*.

Pupa Coloradensis, Cockerell.

Shell brown, shiny, thinnish, striate, especially on penultimate whorl; outline oblong-oval, barrel-shaped; apex blunt; whorls 4; aperture pyriform; peristome brown, thick, continuous by a well marked callus on parietal wall; outer lip not constricted. The teeth within the aperture are brown, one long, one on parietal wall, one on columella, and two (the lower one largest) on outer wall. Long. 1½, lat. 1 mm. Allied to *P. corpulenta*, but decidedly smaller, more striate, and slightly narrower. (Cockerell.)

Pupa Pilsbryana, Sterki.

Shell minute, narrowly perforate, cylindrical-oblong to cylindrical, somewhat attenuated towards the rather blunt apex, colorless (when fresh glassy) with a very delicate bluish tint, smooth and polished, with few, irregular microscopic striæ which are more marked near the aperture. Whorls 4½–5½, moderately rounded with a rather deep suture, especially in the upper half, regularly and slowly increasing, the embryonal being relatively large, the last somewhat ascending toward the aperture; the latter of moderate size, lateral, subovate, margins approached, peristome somewhat expanded, without a thickened lip or a callus in the palatal wall; outside is a barely perceptible trace of a crest near the margin, and behind that a slight impression most marked upon the inferior palatal fold. Lamellæ 4 or 5; one apertural, rather high, of moderate length, simple; one columellar, horizontal, of moderate size, simple; basal very small or wanting; palatals the typical, inferior deeper seated, of moderate size, superior small or very small. Alt. 1.5–1.7, diam. 0.8–0.9 mm.

Pupa Pilsbryana, Sterki, The Nautilus, Vol. III. p. 123, March, 1890.

There is a slight variation; the example from New Mexico being of lesser diameter, and having no trace of a basal lamella.

The soft parts have not been seen so far, but will be of high interest, since, to judge from the shell, our species seems to be an intermediate form between the *hordeacella*, etc. group, and *P. curvidens*, especially its var. *gracilis*.

P. Pilsbryana has much resemblance in shape and size to small albino examples of *P. hordeacella*, Pilsb., but under a glass is at once distinguished by the shorter simple apertural lamella not ending at or very near the upper termination of the palatal margin, as it does in *hordeacella*, and by the smooth surface. The fine bluish hue may also be a distinguishing character if it prove constant.

The above is Sterki's original description.

Pupa calamitosa.

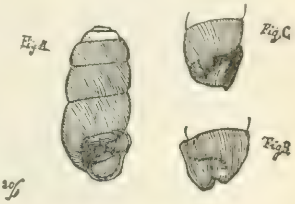
Plate II. Fig. 1.

See 3d Suppl., p. 219. A reduced copy of one of the original figures is given here.

Pupa Hemphilli, Sterki.

In examining a lot of about forty-five specimens of *Pupa calamitosa* from the banks of San Tomas River, Lower California, I found there were two distinct forms in them. The author says, in his description of *P. calamitosa:* "Several specimens have only one lamella on the outer lip, and are rather larger than the typical form described," represented in Plate XII. Fig. 16 (*loc. cit.*, No. 7). Probably I had a greater number of examples at disposition than Mr. Pilsbry. The two forms proved to be distinct by an entirely different formation of the lamellæ, as well as of the basal part of the shell. And among the whole number I found not one intermediate or doubtful specimen. There is no doubt but that we have to consider them as being specifically distinct, the more so since they live together in the same locality. For the new species I would propose the name *P. Hemphilli*, in honor of the man to whom we owe so many valuable additions to our malacological fauna.

As in shape and general appearance the two species are almost alike, it may be the best way to characterize the one in question by comparing it with *P. calamitosa*, Pilsb. *P. Hemphilli* averages a trifle larger than its companion, but either is somewhat variable in size. While *calamitosa* has a minute perforation, *Hemphilli* is umbilicated in quite a peculiar way. There is a nodule-like projection on the umbilical part of the last whorl, producing a rima beside the umbilicus; in *calamitosa* there is nothing of this formation. On the other hand, the latter has a small but distinct groove-like impression just at the base, near the aperture appearing as a slight projection inside. This feature is wanting in *Hemphilli*. Lamellæ: in the latter species, when looking from front, only one is generally seen in the palatal wall, corresponding to the superior one in *calamitosa*, but longer; i. e. beginning deeper in the throat, and fairly seen on the outside; also marked there by a corresponding impression, ascending in a curve from near the base. A little distant from its inner end, just above the projection mentioned, there is another lamella beginning, directed toward the base and ending there, also seen on the outside. Quite generally there is a very small, thin, but well formed lamella in the palatal wall, near the projecting auricle. The columellar fold is quite short and small in *Hemphilli*, yet consisting of a vertical and a horizontal part. The (main) apertural lamella is decidedly longer in our species, and the supra-apertural higher and entire, while in *calamitosa* it is evidently composed of two parts marked by an indentation in the middle, or even entirely separated, in quite mature specimens.



About twenty examples, collected at San Diego, Cal., by Mr. Hemphill, are all *P. Hemphilli*, no *calamitosa* among them. They are little different from the San Tomas River specimens, except by a somewhat shorter palatal lamella.

The above is Sterki's description (The Nautilus, July, 1870, Vol. IV. p. 27). My figure was drawn by him from the type.

Pupa hordeacella, Pilsbry.

Plate II, Fig. 2.

The shell is of a long-ovoid shape, smaller and slenderer than *P. servilis*, Gould, translucent, waxen white, finely striate; the aperture is rounded, with a thin, expanded peristome. Within, there is, on the parietal wall, an entering fold arising near the termination of the outer lip, its edge a trifle sinuous or nearly straight; the columella has a fold about in the middle. There is a tiny deep-seated fold on the base of aperture, near the columella, an entering fold within the outer lip, equidistant from the above described parietal and columellar folds, and a tiny denticle above it. The columellar fold is not situated so high on the pillar as in *P. servilis.* The latter half of the body whorl is flattened on the outer lower portion, as the Figure J shows. There is a low wave-like ridge or "crest" also, but scarcely visible in many specimens. Alt. 1.8, diam. 8 mm.

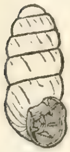
Pupa hordeacella, Pilsbry, Proc. Acad. N. Sci. Phila., 1890, p. 44, Plate I. Figs. G, H, I, J, K.

Arizona to Florida.

The figures were drawn with the aid of the camera lucida. They should be compared with Gould's excellent figures of *P. servilis* in the Boston Journal of Natural History, Vol. IV., Plate 16, Fig. 14, and those of *P. pellucida*, in Strebel's Beitrag zur Kenntniss der Fauna mexikanischer Land- und Süsswasser-Conchylien, Theil IV. Plate XV. Fig. 10. The latter are the more valuable in this connection, as they are not only faithful drawings on a sufficiently large scale, but are the only ones drawn from continental specimens (Vera Cruz, Mexico). The measurements given by Strebel and Pfeffer are, alt. 2½, diam. of last whorl fully 1 mm., alt. of aperture ⅔ mm. Gould's *P. servilis* and Pfeffer's *P. pellucida* were both described from Cuba. I see no reason for not following W. G. Binney in considering them synonymous, *pellucidus* having precedence. (Pilsbry.)

The above is Pilsbry's description. I give also a reduced view of one of his figures.

Pupa Clementina, Sterki.



Pupa Clementina.

Shell very minute, narrowly perforate, cylindrical, pale horn-colored, transparent, with rather obtuse apex; whorls 5½, regularly increasing, moderately rounded, with rather deep suture, smooth, with few microscopic striæ, somewhat shining; last whorl occupying rather more than two fifths of altitude, somewhat ascending to the aperture, with a slight, revolving impression on the middle of its last one third, ending at the auricle; a very slight, flat crest elevation near the margin, only in the lower part; aperture lateral, scarcely oblique, subovate with the palatal margin slightly flattened, upper part of same somewhat sinuous, peristome a little expanded with a slightly thickened lip just at the margin; lamellæ 6, white, two on the apertural wall, the apertural typical, and a rather long supra-apertural, ending in a callus at the upper termination of the palatal margin; columellar one typical, horizontal; basal very small, nodule-like, deep-seated; palatals two, typical, the inferior a little longer. Alt. 1.9, diam. 0.8 mm.; apert., alt. 6, diam. 0.5 mm.

Three examples of this species were collected by Mr. H. Hemphill on San Clemente Island, California, among numerous *P. Californica*, Row. All were exactly alike, well formed and fully mature. They cannot be referred to any one of our species published, and doubtless represent a form of their own, although so far it was not possible to examine the soft parts.

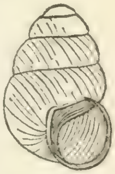
In size, shape, and general appearance it somewhat resembles *Isthmia*, yet lacks the rib-like striation; the lamellæ would be typical for *Vertigo* and some of the smaller *Pupæ* but for the presence of the well developed supra-apertural which *P. Clementina* has in common with *P. calamitosa*, Pilsbry, and *Hemphilli*, Sterki; but, on the other hand, there is nothing of the characteristic palatal or gular folds of these two species. Thus, in several regards, our form is an intermediate and connecting one between different groups, and consequently deserves our special interest.

Pupa Clementina, Sterki, The Nautilus, Vol. IV. No. 4, Plate I. Fig. 4, August, 1890.

The above is a copy of Sterki's original description and figure.

Pupa Dalliana, Sterki.

Shell conic or ovate-conic, of greenish horn-color, transparent, finely irregularly striate in the lines of growth, polished; whorls 4½, well rounded, with deep suture rather rapidly increasing, the last occupying about ⅗ of altitude towards the aperture, somewhat ascending on the penultimate. Aperture lateral, somewhat oblique, subovate, with just perceptibly flattened palatal margin; margins approximate, the ends protracted; peristome shortly but decidedly expanded, with a very fine thread-like lip near the margin, the same continuing as a very fine callus on the apertural wall inside of the line connecting the ends of the margins; palatal wall quite simple; no lamellæ. Alt. 1.2, diam. 1.3 mm.



Pupa Dalliana.

This form has been collected by Mr. Hemphill near Clear Lake, Lake Co., Cal., and I propose to name it in honor of Mr. William H. Dall. The specimens before me were fifteen, fresh, remarkably uniform in their whole appearance; all were more or less covered with a dark brown hard crust of slime and dirt, generally thickest around the aperture. Doubtless this coating is done "purposely" by the animals, as in many other species also. When cleaned, it shows about the size and shape of a well grown *Vertigo ovata*, Say; but by a good eye, or under a glass, is at once recognized as something else, by the rounded aperture and the absence of lamellæ. (Sterki.)

Pupa Dalliana, Sterki, The Nautilus, Vol. IV. No. 2, p. 19, June, 1890.

Dr. Sterki's description is copied above. My figure was drawn by him from the type.

Pupa syngenes, Pilsbry.

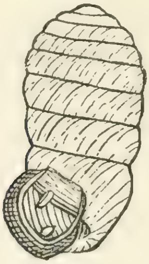
Shell subcylindrical but wider above, composed of eight narrow, convex whorls, *sinistrally convoluted*: texture as in *P. muscorum*, but color rather lighter brown. Last whorl ascending, imperforate, bearing a strong high crest just behind the outer lip. Aperture shaped as in *muscorum*, having a single small parietal denticle. Altitude 3¾, diameter 1⅔ mm.

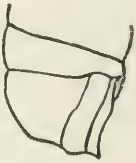
Pupa syngenes, PILSBRY, The Nautilus, 1890, Vol. III. p. 296, Plate V. Figs. 1, 2.

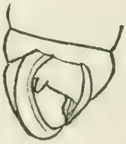
Two specimens of this form are before me, and I am in doubt whether to give them a new name, as they may be only sinistral monstrosities of the common *P. muscorum*. The shells are labelled "Arizona" in the Academy collection, collector not known.

(Since the above paragraphs were in type, I have received a communication from my friend, Dr. V. Sterki, to whom I sent a specimen of *P. syngenes*, which I at first described as a variety of *muscorum*. He says: —

"I am satisfied that it is a species, and not a var. of *muscorum*; the shape of the whole shell, the last whorl so considerably flattened, and ascending, the number of whorls, seem to me to prove its specifical rank. . . . After washing out the aperture of your specimen, I saw a rather strong lamella or tooth on the columella, and a barely perceptible trace of an inter-palatal lamella, which, however, is validified by the impression on the outside.")







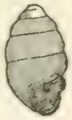
The above is Pilsbry's description. An authentic specimen drawn by Dr. Sterki is figured here.

Vertigo ovata, SAY.

Of *V. tridentata* Sterki writes (The Nautilus, 1890, p. 135): "It has a wide distribution in the northern part of the country; originally found in Illinois, it has been collected in different parts of Ohio and New York, as well as in Minnesota and Colorado. In general it is remarkably constant in its characters; yet there are slight differences; here I found a few examples from low ground, together with *V. ovata;* they were a trifle larger, with a thicker and deeper colored shell than those from upland places."

Vertigo Oscariana, Sterki.

This is the most peculiar of our species. It is of the size of *milium*, but oblong, with either end nearly equally pointed, the last whorl being considerably narrowed and flattened towards the subtriangular, small aperture; shell thin, delicate, of pale horn-color, as is the palatal wall and margin; the latter simple and straight, with a very slight, thin callus inside; lamellæ 3, whitish, rather small; one apertural, one columellar (longitudinal), and the inferior palatal; sometimes there is also a very small superior palatal. Length 1.5, diameter 0.8 mm.



V. Oscariana. $\frac{20}{1}$

This remarkable *Vertigo* has been detected in Eastern Florida, on the coast at Mosquito Island, etc., by Mr. Oscar B. Webster and his father, Mr. Geo. W. Webster, of Lake Helen, Florida. These gentlemen took much pains to ascertain the range of distribution of this form and some others, and it is consequently only just to name the species in honor of Mr. Webster. The most striking character of it, besides the narrowed last whorl, is the thin and straight palatal wall and margin, so that, indeed, the shell appears to be immature. But when seen under a glass of sufficient power, the margin is completed, and, as already mentioned, there is a thin callus at a little distance from the margin. Moreover, Mr. Webster wrote me that, of more than 150 examples he had seen, all were alike.

A few days ago, in a lot of *P. corticaria*, Say, from Ithaca, N. Y., sent from Texas, there was one example of this species, the shell dead, but in fair condition, a little larger and less fragile than the Florida examples, and with a well marked callus corresponding to a slight but distinct crest. The specimen may have been collected in New York, and from its appearance at least I would ascribe to it an origin north of Florida. Since the above was written, I have found a few examples in drift from Guadalupe River, Texas, collected by Mr. J. A. Singley, sent by Mr. Wm. A. Marsh.

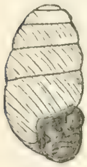
By the kindess of Mr. Webster I was enabled to see a living example. The foot and the lower parts of the head are nearly colorless; head, eye-tentacles, and neck light gray. Jaw very tender, thin, pale yellow, consisting of about 14 longitudinal plates, shorter and wider in the middle, longer and narrower toward either end; it is much like that of *V. tridentata*, Wolf. Odontophore about 0.36 mm. long, 0.1 mm. wide, about 110 square rows in each $\frac{m}{3}+\frac{9}{3}+\frac{x}{4}$ teeth; central very small; laterals gradually passing into marginals; the latter serrate. Different from that of *V. tridentata*.

In drift with numerous minute shells, from Guadalupe River, Texas, kindly sent by Wm. A. Marsh, I found one specimen of this species, which consequently is not confined to Eastern Florida, where it was detected by Messrs. Webster, but may be widely spread over the southern part of our country.

Vertigo Oscariana, Sterki, Proc. Ac. Nat. Sci. Phila., 1890, p. 33; The Nautilus, 1890, p. 136.

The above is Sterki's description, and the figure is drawn by him from the type.

Vertigo Binneyana, Sterki.



V. Binneyana. $\frac{20}{1}$

They are of the size and general appearance of *V. callosa*, very narrowly perforate, cylindrical oblong, light chestnut-colored; whorls 5, moderately rounded, nearly smooth; aperture relatively small, peristome little expanded; outer wall with a well formed crest interrupted by a rather long revolving groove; corresponding to the crest there is a callus of lighter color; lamellæ 6; on the apertural wall a small supra-apertural and a well developed apertural; columellar appearing rather massive; at the base, one rather small but well formed, appearing tooth-like; palatals 2, long, especially the inferior. Length 2.0 mm., diameter 1.0 mm.

Last year, Mr. W. G. Binney kindly presented me with two examples of a *Vertigo* collected at Helena, Montana, by Mr. H. Hemphill, which seemed to be of a new species; but yet I did not like to publish a description founded upon only these two specimens. Lately among a number of small *Pupidæ* from different parts of British America sent by Mr. Geo. W. Taylor of Ottawa, there were a few examples of this same species, from Winnipeg, Manitoba, dead and weathered, but good enough to be identified.

Probably there are other examples of this species in collections, and more will be found in the Northwest. It is named in honor of Mr. W. G. Binney, to whom I owe the two beautiful specimens in my collection.

Vertigo Binneyana, Sterki, Proc. Ac. Nat. Sci. Phila., 1890, p. 33.

The above is Sterki's description. I am also indebted to him for the figure.

Vertigo callosa, Sterki.

There are in collections two different species under the name of *V. Gouldii*, Binn. Their size and coloration is nearly the same, at least in most variations, as are also the apertural lamellæ as to number and position. Yet they are decidedly and constantly distinct, especially by the formation of the outer wall at the aperture. Judging from the descriptions and more especially from the figures, the true *V. Gouldii* is the one characterized as follows: the last whorl is somewhat predominating, thus rendering the whole shell more ovate or conic ovate; the palatal wall near the aperture is decidedly flattened, or impressed, the impression comprising also the crest and being especially well marked at the "auricle" (as I name the more or less projecting part about the middle of the outer margin, to have a concise expression), forming a roundish groove outside and a decidedly prejecting angle inside, thus producing the "two curves meeting in the centre of the peristome." A feature not striking, but only seen by careful examination, is the position of the short tooth-like lamella at the base, somewhat nearer the margin than the end of the columella, the base perceptibly widened at that place; the said lamella is probably an equivalent of the inferior columellar lamella, which in most *Vertigos* stands very low, in many exactly at the base.

The other species, *V. callosa*, has the last whorl relatively less wide, so that the whole shell is of a more oblong shape. In the palatal wall, only the part behind the crest is somewhat flattened, while the latter itself forms one unbroken curve from the base up to the suture, and at the moderately projecting auricle there is only a slight flattening. The inferior columellar lamella is at the end of the columella, sometimes wanting or a mere trace. Well worthy of notice is a peculiar formation of the surface, the epiconch showing microscopic wrinkles or foliations in the direction of the lines of growth producing a peculiar silky gloss, especially on quite fresh examples, and more in some forms than in others.

The first two examples of this species I obtained in 1885 from Mr. Henry Moores, of Columbus, Ohio, and in 1889 I saw a few more in his collection. In 1887, Mr. E. W. Roper sent me some others from Massachusetts. Last year in different collections I saw quite a number of specimens from different places in New York near the metropolis, under various names: *V. Gouldii*, *milium*, *ovata*, and also mixed with *Bollesiana*. Of the Ohio examples the color is somewhat lighter, the callus and the lamellæ are strong and white, while in the Eastern examples they are somewhat thinner and more of the color of the shell. The name *callosa* was thus mainly derived from the Ohio form (which, however, may be regarded as a variety).

It is with some hesitation, however, that I now bring it under this head; it is the equivalent of the European *V. pygmæa*, Drap., of which I have examples for comparison from different countries of the Old Continent, which I have partly collected myself there during a number of years. The two may even be identical; at least it would be absolutely impossible to distinguish New York examples from most Europeans. Both forms agree also in certain variations of the apertural lamellæ; the inferior columellar lamella may be absent in either, or there may be present a small supra-palatal fold, thus rendering the number variable from 4 to 6, the typical, however, being 5. An examination of the soft parts will probably decide the question; so far I have not had an opportunity to make it.

On our continent, the range of distribution of the two species — *V. Gouldii* and *callosa* — seems to be somewhat different, the former having been found in New York, Ohio, Illinois, and Colorado, the latter from Massachusetts to Ohio.

Vertigo callosa, Sterki, Proc. Ac. Nat. Sci. Phila., 1890, p. 31.

The above is Sterki's description.

Vertigo parvula, Sterki.

Among several hundred small *Pupidæ* collected in Northeastern Ohio (Summit and Lake Counties) by Mr. A. Pettingell, there were two examples of a doubtless new species, which I in the same way named *V. parvula*. It is about of the size, shape, and appearance of *V.* (*Angustula*) *milium*, Gould; but ranges in quite another group, having a quite simple palatal wall and margin, and only three lamellæ.

In Texas, *Vertigos* seem to be decidedly rare. In many hundreds of *Pupidæ* from that State which Mr. J. A. Singley and Mr. Wm. A. Marsh kindly forwarded me there were only about half a dozen such; a few *milium*, one *rugosula*, one *Oscariana*, as mentioned above, and one specimen of a form which probably will prove to be a new species of quite peculiar formation.

Vertigo parvula, Sterki, The Nautilus, 1890, p. 136.

The above is Sterki's description.

Vertigo approximans, Sterki.

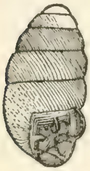
In 1887, Mr. A. A. Hinkley, of Dubois, Ill., sent me, with other *Pupidæ*, one specimen of a *Vertigo*, probably new, and in 1889 another of the same. The said gentleman and Mr. William A. Marsh kindly forwarded me all their *Pupidæ* for examination, but so far I have found no other example, yet I am satisfied such will be found. The form is related to *Vertigo ovata* and *Gouldii*, but different, and is characterized by the two palatal lamellæ being close together, for which reason I gave it the manuscript name *V. approximans.*

Vertigo approximans, Sterki, The Nautilus, 1890, p. 136.

The above is Sterki's description.

Vertigo rugosula, Sterki.

Related to *V. ovata* and *Gouldii;* in shape more elongated than the latter, more cylindrical, and somewhat larger. Apertural parts and lamellæ much like those of *ovata;* but the columella is decidedly longer and straighter, and the inferior columellar lamella is distinctly placed on it. Length 1.8–2.0, diameter 1.1 mm. Of a peculiar formation is the surface. Of the five well-rounded whorls, about one and a half of the upper are nearly smooth; the following, with exception of the last, are distinctively and regularly striated; the last is very finely but distinctly rugose in the sense of the lines of growth, near the aperture again striated. Color, dark chestnut.


V. rugosula.

This is a beautiful species, of which I saw the first example in the collection of Mr. Bryant Walker, who had found it in April last at Pass Christian, Mississippi. Last September, Mr. W. G. Mazyck collected a number of them on Sullivan's Island, S. C. In either place they were in company of *Pupa rupicola,* Say. Quite lately I have seen one example from Lee County, Texas, sent by Mr. J. A. Singley; it was a dead shell, and not fully mature, but recognizable. The species consequently seems to be widely distributed along the South Atlantic and Gulf coasts. Two specimens were sent in by Mr. H. Hemphill, who collected them at Fish Camp, Fresno Co., Cal.

In Eastern Florida, Volusia County, etc., a form has been found to be quite common which I refer to this species, but as a distinct variety which may be called *ovulum.* It is somewhat smaller, ovate; the striation and rugosity of the surface are less marked, and the inferior apertural lamella is wanting. In turn it has in most examples a lamella at the base (between inferior columellar and inferior palatal), and the callus in the palatal wall is rather strong. The coloration of part of them is somewhat lighter. It cannot be confounded with *V. ovata,* Say, its relations to the type of *rugosula* being evident, and, in addition, *ovata* has been found with it. Nor can it be referred to *ventricosa.* It is larger and stronger, of much darker color, its surface is not so smooth and polished, it has three or even four lamellæ more, and the columella is longer.

Vertigo rugulosa, Sterki, Proc. Acad. N. Sci. Phila., 1890, p. 34.

The above is Sterki's description. The figure was drawn by him.

Liguus fasciatus, Mull.

Plate I. Fig. 5.

The Vaccas Key variety, noticed in page 435 of the Manual of American Land Shells, is figured in the plate.

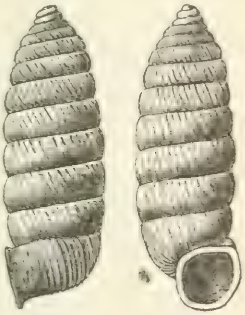
Orthalicus undatus, Brug.

Plate II. Fig. 4.

I give a new figure of the variety of this species.

Holospira Arizonensis, Stearns.

Shell dextral, elongately cylindrical, pupiform, dingy white to pale horn-color, translucent. Number of whorls, twelve to thirteen. Slightly convex, the sutures distinctly defined. The upper six or seven whorls rather abruptly tapering towards the obtuse apex, which has a slightly twisted and rather a papillose aspect. The last whorl is curved under and constricted back of the mouth, forming an umbilical notch. The apex and following whorl are smooth; the three or four succeeding whorls sharply and somewhat obliquely plicated longitudinally, the median and following whorls becoming somewhat obscurely sculptured other than by distinct growth lines. The basal whorl is strongly sculptured below, and back of the mouth, and obtusely angulated underneath. Aperture ovate, slightly angulated anteriorly, somewhat effuse, rimmed and projecting. The dimensions of two examples are as follows: —



	mm.
Longitude	12½
Longitude	13
Greatest diameter	4
Greatest diameter	4

Dos Cabezas, Arizona, where the above two specimens and numerous fragments were found in a cave in November, 1889, by V. Bailey, and contributed to the United States National Museum (No. 104,392) by Dr. C. Hart Merriam.

Among the species of this group that are geographically related is *H. Remondi*, Gabb, described from Arivechi, Province of Sonora, Mexico, a form sharply sculptured throughout, and in minor features also different; *H. Pfeifferi*, Menke, collected by Remond at Hermosillo, in the same province, with the previously named species; and *H.* (*Cœlocentrum*) *irregulare* of Gabb, from the high table-lands back of Mulege, in the peninsula of Lower California. All of these are separable at a glance from *Arizonensis.*

The above is Stearns's description and figure from Proc. U. S. National Mus., Vol. XIII. p. 208, Plate XV. Figs. 2, 3, 1890.

Onchidella borealis, Dall.

Coos Bay, Oregon.

It is gregarious in its habits. Fifty specimens were taken in a small crevice of clay shale, near high tide. Single individuals, or several clustering together, were taken afterwards lower down on the tide under loose stones. When in motion, the animal moves off quite rapidly for so small a creature, with two short, stout peduncles protruding in front of the mantle, bearing keen, sharp black eyes. The color is dark slate, splashed with blotches and streaks of ashen white. The body when in motion is $\frac{1}{2}$ inch long, $\frac{3}{16}$ wide, $\frac{1}{8}$ high, and oblong-oval in form, a little broader behind than before. It is covered with small tubercles, which are larger around the edge of the mantle than those higher up on the body, giving the edge of the mantle a serrated or tooth-like appearance when the animal is at rest. When it is at rest on a smooth surface, the base of the animal is nearly circular, or a little longer than wide, the centre of the body is elevated to quite a sharp apex, which together with its color resembles some varieties of a very young *Acmæa pelta*, and would be very readily taken for such by an inexperienced collector. The foot is white, and works in rapid undulations when the animal is in motion.

The above remarks are made by Mr. Hemphill in a recent letter.

EXPLANATION OF PLATES.

PLATE I.

Fig. 1. Anadenus Cockerelli. Animal and internal shell.
Fig. 2. Patula strigosa, var. Buttoni.
Fig. 3. Arionta ruficincta.
Fig. 4. Glandina decussata, var. Singleyana.
Fig. 5. Liguus fasciatus, var. from Key Vaccas.
Fig. 6. Bulimulus Dormani.
Fig. 7. Arionta Ayersiana.
Fig. 8. Zonites Simpsoni, enlarged.
Fig. 9. Binneya notabilis, enlarged.
Fig. 10. Same as Figure 2, toothed variety.

PLATE II.

Fig. 1. Pupa calamitosa, reduced from original figure.
Fig. 2. Pupa hordeacella, from original figure.
Fig. 3. Selenites Duranti, var. Catalinensis, enlarged.
Fig. 4. Orthalicus undatus, variety.
Fig. 5. Selenites Vancouverensis, var. Keepi, enlarged.
Fig. 6. Triodopsis Mullani, var. Blandi.
Figs. 7, 8. Arionta tudiculata, var. cypreophila.
Fig. 9. Bulimulus Ragsdalei, enlarged one half.

PLATE III.

Fig. 1. Limax Hemphilli, var. pictus. Animal and internal shell.
Fig. 2. Zonites Diegoensis, enlarged.
Fig. 3. Zonites macilentus, enlarged.
Fig. 4. Tebennophorus Hemphilli, jaw.
Fig. 5. Anadenus Cockerelli, jaw and tongue.
Fig. 6. Pristiloma Lansingi, enlarged.
Fig. 7. Zonites Caroliniensis, enlarged.
Fig. 8. Helicodiscus fimbriatus, var. salmonaceus, enlarged.
Fig. 9. Zonites sculptilis, enlarged.

PLATE IV.

Fig. 1. Arionta Kelletti, var. multilineata.
Fig. 2. Arionta Kelletti, var. nitida.
Fig. 3. Arionta Kelletti, var. albida.
Fig. 4. Arionta Kelletti, var. castanea.
Fig. 5. Euparypha Tryoni, var. nebulosa.
Fig. 6. Euparypha Tryoni, var. fasciata.
Fig. 7. Patula strigosa, var. bicolor.
Fig. 8. Patula strigosa, var. lactea.
Fig. 9. Patula strigosa, var. albofasciata.

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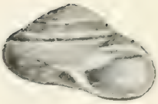
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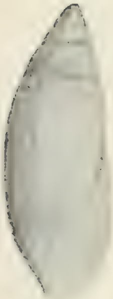
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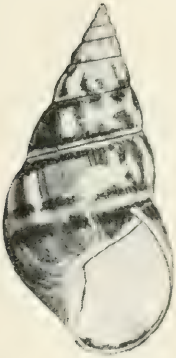
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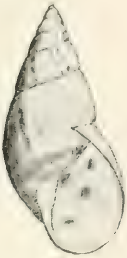
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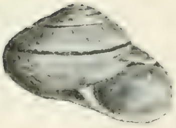
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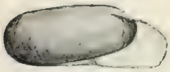
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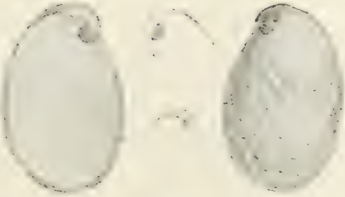
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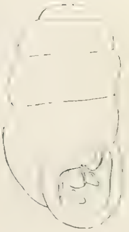

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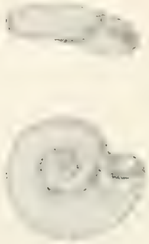

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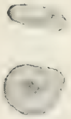

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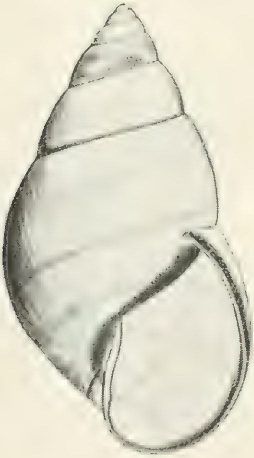

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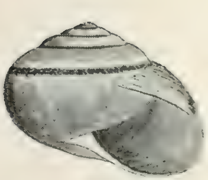

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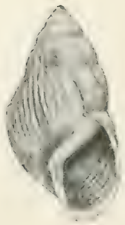

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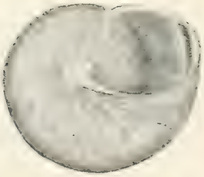

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